PHENO-MORPHOLOGICAL STUDIES OF SELECTED TREE SPECIES IN A TROPICAL FOREST ECOSYSTEM

By

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THESIS

Submitted in partial fulfilment of the requirement for the degree

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Faculty of Agriculture
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Department of Tree Physiology and Breeding
COLLEGE OF FORESTRY
VELLANIKKARA, THRISSUR

1994

Dedicated to My Parents

for all I am today and hope to be in future

DECLARATION

I hereby declare that the thesis entitled **Pheno morphological Studies of Selected Tree Species in a Tropical Forest Ecosystem** is a bonafide record of research work done by me during the course of research and that the thesis has not previously formed the basis for the award to me of any degree diploma associateship, fellowship or any other similar title, of any other University or Society

Vellanikkara
28 11 1994

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CERTIFICATE

Certified that the thesis entitled **Pheno morphological Studies of Selected Tree Species in a Tropical Forest Ecosystem** is a record of research work done independently by **Mr Gopakumar, S** under my guidance and supervision and that it has not previously formed the basis for the award of any degree fellowship or associateship to him

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Introduction

INTRODUCTION

Human interest in plant life dates back to the prehistoric times Apart from being a significant ecosystem counterpart plants are a source of his daily needs With the advent of agriculture the pulse of plant life with the seasons has captured man s curiosity This inquiry into life s subtle signals and responses progressively gained importance and became decisive in determining the success or failure of his crops

Plant pheno morphology deals with the study of temporal changes in the morphology of plants over a specific period Simply it is the study of the visible life history of each of the vegetative and generative organs of the plant (Orshan 1989) Pheno morphology combines the uses of phenology which deals with the seasonality of phenophases and of morphology

A lot of emphasis is being laid for the conservation of tropical biodiversity as it has become essential for the survival of the human race But a thorough knowledge of tropical plant life is lacking The numerous yet unique relationships which exists between plants and their environment in a forest ecosystem are seldom recognized It is important to understand how these systems are organized biologically and how they respond with their biotic and abiotic environments Such an understanding will help in the successful management of these valuable natural resources

Seasonal changes in plant growth and development are decisive in determining the plant s adaptation to a changing environment Their importance increases with the magnitude of variation and the intensity of stress periods The variation in the developmental dynamics of plant organs in different seasons are also important variables in adaptation when some factors are limiting

Equally important are the organization studies of tropical tree species Trees are not static objects They are dynamic organisms constantly growing and becoming more elaborate The continued construction is represented by progressive accumulation and loss of morphological features in an organised and flexible manner controlled by proximate and ultimate factors The precise constructional principles upon which each species arrange their different organs and regulate their growth yields more information on their developmental dynamics It is important to know where and when each part of the plant originates and starts growing and how it responds to changes in the immediate environment and how it contributes to the final form of the plant

This study was taken up to clearly understand the seasonal growth cycles of some selected tropical tree species found in the moist deciduous and semi evergreen tracts of the Trichur Forest Division Further to elucidate the fascinating array of external structures that these species present to the environment

Review of Literature

REVIEW OF LITERATURE

Periodic behaviour of plants in tropical environments has received little attention With regard to tropical forests none of the earlier investigations were oriented towards the unification and analysis of periodicities for leaf, flower and fruit of nearly all the plant species of which a particular forest type is composed

The study of phenology in tropical ecosystems is important if we are to learn more about the dynamics of plant species It is necessary to study first how species operate within the context of their respective environments (Lieth 1974) Relationships that evolve between a species and its abiotic and biotic environment may vary from one section of its geographic range to another

2 1 Phenology

2 1 1 Preliminary works

Much information on the phenodynamics of trees have been obtained from both the seasonal and aseasonal forests (Croat 1969 1975 Frankie et al 1974 Gentry 1974 Janzen 1967) In the humid tropics also works by Ashton (1969) Burgers (1972) Holmes (1942) Koelmeyer (1959) and

Sasaki et al (1980) throws much light on tropical tree phenology More investigations of the phenological patterns of the seasonal tropical forests includes those by Boaler (1966) Burger (1974) Croat (1969) Daubenmire (1972) Foster (1973) Fournier and Salas (1966) Hopkins (1970) Nevling (1971) Opler et al (1976) and Smythe (1970) Hilty (1980) has monitored and accounted the flowering and fruiting patterns in a premontane rainforest in Pacific Columbia

Studies in more or less aseasonal climates are limited to those by Corner (1952) Koriba (1958) McClure (1966) Medway (1972) Ng (1977) Baker and Baker (1936) Brookfield (1969) and Frankie et al (1974) The drawback associated with all these studies is that they are not based on systematic observations of large number of trees growing in their natural environments and also are sometimes based on surveys of herbarium materials

2 1 2 Significance in forestry

The patterning of phenological events of forest trees can have important practical implications for forestry Mahadevan (1991) stated that phenological observations on tree species could be effectively utilized as an aid to seed collection He reported a noticeable tree to tree variation within a selected number of species as regards fruit maturation and seed ripening As most tropical tree seeds have a very short dormancy seed supply is sporadic So knowledge of these events helped in effective harvesting of these invaluable propagules

Information on the differences between sympatric populations of morphologically similar entities in aspects such as reproductive phenology and pollination biology combined with evidence for outbreeding and for interspecific hybridization in nature assisted in evaluating whether such entities behave as biological species (Ashton 1988)

Phenology is a relatively underdeveloped science but its significance as an information processing subject should not be overlooked In recent years it is seen to have a major practical role in the conservation of tropical plant diversity Riabinin (1978) introduced a number of well defined general and new concepts into this theory with explanatory diagrams by referring to various elements in the landscape

Dhamanitayankul (1979) used the phenological observations carried out in a dry evergreen forest in north east Thailand to schedule logging operations The logging operations were recommended after seed shedding by the trees

Mulik and Bhosale (1989) listed out the usefulness of phenological studies According to them these studies were helpful in combating afforestation and in plant management honey analysis floral biology and in estimation of reproduction and rege cration

Seasonal cycles in plants do have a relationship with seasonal cycles in animals Investigations by Pandey et al (1988) in the Kanha National Park revealed that phenological stages of plant species show their specific relationship between seasonal availability of food seasonal utilization pattern and movement of ungulates and consequently their distribution in the study area

Beniwal (1987) stressed that phenological data are important for timing seed collection and raising nursery plants and plantations

2 1 3 Flowering patterns in trees

In the tropics flowering of forest trees are quite often irregular A brief review of flowering of tropical plants was made by Bawa (1983) The evergreen forest flowering phenology had been subjected to a series of inventories by Pinto (1970) Ng and Loh (1974) Cockburn (1975) and Ng (1975 1981) Also Lee (1971) attempted to study the reproductive biology of a tropical forest as a whole entity

Floral bud initiation development blooming and floral persistence comprise the phenomenon of flowering (Borchert 1983 Ratheke and Lacey 1985) The floral biology though much significant has not been thoroughly studied

There is a marked variation in the frequency time and duration of flowering Not all trees flower in a similar manner Even individuals of the same species exhibit marked variations Bawa (1983) and Primack (1985) reported that this variability can be seen even in populations and ecosystems and also according to the climatic conditions

Clark and Myer Scough (1991) in their study of the reproductive phenology of Avicenia marina in south east Australia found out that flowers of individual trees varied greatly between years and many trees failed to reproduce each year although the population remained fecund from year to year Flowering phenology of an African riverine forest ecosystem was found to be highly variable over times resulting in community wide periods of relative resource abundance and scarcity (Kinnaird 1992)

Lampe (1992) on observing phenophases in tropical semi arid vegetation of northern Venezuela concluded that flowering of trees and tall shrubs occurred at the end of the dry season and lasted throughout the entire rainy season The short duration rains late in the dry season according to her may have triggered and synchronised flowering

Baker *et al* (1983) reported that the flowering frequencies in the Costa Rican forests followed a bimodal distribution Gregarious flowering of south Asia Dipterocarpus forests has been widely authenticated Medway (1972) and Janzen (1974) reported that dipterocarps flowered synchronously once in 5 13 years

In India the principal tree species, teak has been subjected to extensive phenological observations Its flowering phenophases were studied by many workers (Nanda 1962 Dabral 1976 Ramprasad *et al* 1990) Sahai and Tandon (1993) reported that there is a marked variation in flowering patterns of teak and is quite pronounced within and between trees

In most tropical trees flowering is an episodic event and seasonal peaks have been recorded for many tropical forests (Fournier and Salas 1966 Janzen 1967) The periodicity with which a tree flowers is very much dependent on competition of pollinators pollinator activities and selection of life history traits (Bawa 1983 Primack 1985)

While there are some trees in flower and fruit all time most species bear fruit and flower only periodically many of them annually and that some years are better than others

In contrast to the herbaceous plants flower development in many trees is not continuous from flower induction to anthesis but may become temporarily arrested at some intermediate stage Final development of flower buds and anthesis will occur many months after flower initiation This functionally important topic has not been considered adequately in many discussions of flowering in trees (Halle et al 1978)

An individual s flowering pattern is defined by the duration of flowering as well as number and temporal distribution of flowers Among tropical species the flowering phenology of individual plants varies continuously between two extreme patterns (Janzen 1971 Heinrich and Raven 1972 Gentry 1974) At one extreme are species with mass flowering individuals producing large number of new flowers each day over a week or less At the opposite extreme are species with steady state individuals producing small numbers of new flowers almost daily for many weeks Okada (1990) observed various types of flowering phenophases within Polyalthia littoralis in the Bogor Botanic Gardens Indonesia

Phenological studies in an Oak forest type revealed a unimodel (spring) flowering curve most characteristic of broad leaved forest the seasonal (summer) peak is characteristic of species growing in marginal and cleared areas (Mitina 1976) Tamarina (1976) identified two main flowering seasons for dipterocarps with a flowering to fruiting period of 2 5 months

Donosco (1975) had quantified information on the phenological aspects of four species of Nothofagus in Chile Jindal and Solanki (1985) observed the flowering rhythms of Tecomella undulata They observed that the species started flowering in November and continued until the end of March Flowering was asynchronous and lasted 59 103 days Peak flowering occurred from the end of February until the middle of March and lasted 9-19 days Flowering patterns of three species of Melicytus in New Zealand has been outlined by Powlesland et al (1985) The flowering phenology of tropical plants has been summarised and described with illustrations by Herklots (1977)

Qualitative observations on the flowering pattern of spotted gum in Queensland was done by Dale and Hawkins (1983) The buds matured 10-11 months before flowering Flowering was observed throughout the year although it generally occurred in October January with November being the main flowering month

Studies attempted on the temporal and spatial variation in the flowering phenology of a tropical rain forest by Heideman (1989) revealed that within year variation was low (2 4 fold) relative to other tropical sites while microgeographic variations was high (10 100 fold) However the large differences at the community level were not significant

Jonsonn *et al* (1976) found good agreement in flowering frequencies and phenology between years in a study on the flowering of *Pinus sylvestris* seed orchard

2 1 3 1 Selective factors

Flowering has a strong genetic and micro environmental basis McCarthy and Quinn (1989) argued that the phenomenon of flowering is sensitive to yearly environmental variation A favourable environment at the time of flowering differentiation may result in increased flower production In Ceylon in both the perhumid and seasonally dry forests flowering of forest trees had been shown to follow a period of low rainfall or humidity or both (Koelmeyer 1959 1960)

The timing of flowering in tropical trees usually has been ascribed to environmental control mechanisms analogous to those that have evolved in temperate plants to adapt vegetative and reproductive development to a growing season of limited duration (Larcher 1980)

Endogenous factors and not environmental ones appear to be mainly responsible for flower induction in tropical trees The effect of environmental factors is only indirect through their effect on seasonal vegetative development of trees This view is supported by the fact that most trees must pass through a prolonged juvenile period before acquiring the potential to flower and once mature often do not flower every year (Koelmeyer 1959 Bullock and Bawa 1982)

The variation in peak flowering of seasonal tropical forests as a function of the severity of drought (Fournier and Salas 1966 Janzen 1967) flowering during drought periods in tropical rainforests and the wide temporal range of flowering within individual species as a function of tree water relations suggest a predominant role of seasonal changes in water status as determinants of tree development including flowering (Reich and Borchett 1984)

Considerable controversy exists as to the question what triggers flowering Suggestions exist that a given tree may need a prolonged period of physiological preparations before it is ready to respond to an external stimulus to flower (Wood 1956 Fox 1972) Burgess (1972) was of the opinion that there is considerable circumstantial evidence that gregarious flowering is in some way connected with drought periods occurring 3 5 months before flowering But the final conclusion can be obtained only from the study of individual trees and monitoring the weather they experience Ng (1983) on examination of weather records suggested that the trigger to flowering in dipterocarps was not the onset of drought itself but the concomitant rapid increase in the hours of sunshine as wet cloudy weather was replaced by clear blue skies There was also substantial body of circumstantial evidence that the flowering of many lowland rainforest tree species is promoted by water stress but the relationship was not simple

Studies conducted to evaluate the effect of weather factors on the rhythm of seasonal development of Tilia cordata by Berdinikova and Bulygin (1979) using multiple regression analysis methods found mean diurnal temperature as the main factor governing flowering date

Kulygin (1977) attempted to study the effect of temperature on the flowering times of Robina psuedoacacia and Gleditsia triacanthos He found a close direct relation between the start of flowering of these two species and the sum of effective mean daily temperatures (over +5°C)

For some species of palms according to Windsor _et al_ (1987) canopy openness stimulated flowering The phenodynamics of _Pinus helepensis_ on two different sites in Israel was found to be affected by temperatures (Weinstein 1982)

2 1 4 Fruiting pattern in trees

In tropical forests there exist different types of fruits growing and ripening all the year round However there are fruiting seasons when a higher proportion of species and individuals is in fruit By no means every individual distributes its fruiting periods in the same fashion as with flowering there are instances of long sustained fruit ripening and of regular or irregular dispersal at intervals from a few months to many years Irvine (1961) pointed out that in West Africa fruits of _Terminalia ivorensis_ had been collected from different sites in most months of the year while fruiting of _Claoxylon hexandrum_ was used to mark the onset of a festival These data helped a lot in planning fruit collections but not every flowering event was followed by a fruit crop

Fruiting phenology includes fruit initiation growth ripening fruit fall and the presentation of fruits to dispersers (Rathcke and Lacey 1985) Janzen (1978) had made a comprehensive review of seeding patterns for tropical trees

Continuous fruiting has been observed in *Trema guineensis* (Longman and Jenik 1974) *Trema orientalis* (Stocker 1981) *Cecropia obtusa* (Holthuijzen and Boerboom 1982)

A tree flowering profusely need not always result in fruit In *Hymmanae courbanii* although flowering was an annual phenomenon fruiting was abundant only once in five years Abortion of fruits and immature fruits varying between one to hundred per cent had been recorded (Bawa *et al* 1985) Baker and Harris (1957) reported that in the West African species *Parkia capertoniana* only four to five fruits developed out of the approximately 2000 fertile flowers

Phenological observations carried out by Newton (1988) on moist deciduous forest on the central Indian highlands revealed a fruiting peak in the hot weather and early monsoon for 215 selected sample trees of 61 species Beniwal (1987) reported that in the forests of north east India fruiting was delayed by high temperature and drought

For tropical trees fruiting times can be inconsistent within and between years (Foster 1982) In aseasonal forests in Malaysia intervals between fruiting were often irregular both within and between species (Putz 1979) Individuals of many tropical trees may skip fruiting in some years (Hurlbert 1970 Janzen 1978 Medway 1972)

2 1 4 1 Selective forces

Abiotic factors may influence ripening times and is more concerned with dispersal success In the tropics fruits of *Hybanthus* shrubs atypically produced during the dry season were often abnormally small and contained non viable seeds (Augspurger 1981) In seasonal tropical forests most wind dispersed species ripen and release fruits near the end of the dry season when the trade winds are strong and when many leaves had fallen (Croat 1969 Howe and Smallwood 1982 Janzen 1967 Leiberman 1982 Putz 1979) The dispersal timing also minimizes the time that seeds will lie on the ground before germinating at the beginning of the rainy season (Garwood 1983)

In aseasonal tropical forests in Malaysia where animal dispersers may be available throughout the year fruiting occurred all year around and no fruiting peaks were evident (Putz 1979) In more seasonal tropical forests the number of species with animal dispensed fruits showed a peak of fruit ripening during the rainy season (Janzen 1967 Karr 1976 Lieberman 1982 Terborgh 1983)

Extended ripening duration reflected the seasonal unpredictability or scarcity of resources needed for fruit development (Bawa 1983)

In the species rich tropical rain forest the main factor determining flowering and fruiting times may be the need of individuals within a population to co ordinate their reproduction in order to attract pollinators to effect cross pollination attract fruit dispersers and satiate seed predators (Augspurger 1981 Janzen 1967 Primack 1985) Factors of weather leaf litter and pests in the soil might affect the viability of seeds in the soil and may determine the best time for seed dispersal in temperate species Large seeded indigenous species that lack any seed dormancy such as jack fruit may be under selection to disperse their fruits at the time of year most suitable for germination of these vulnerable seeds

Foster (1982) identified two dispersal peaks for the canopy trees at Panama and a single peak for lianas In discussing the significance of these peaks he concluded that these may be advantageous in the dispersal of seeds which can be done together Flowering trees are also reported to ripen their fruits at the same time irrespective of their initiation to bear ripening fruit at about the some time This can well be a selective advantage in seed dispersal which has been reported by Medway (1972) for Shorea spp

In most tropical forests variation in rainfall appears to be the most significant climatic factor influencing the phenologies of flowering and fruiting (Foster, 1974 Hilty, 1980 Borchert 1983)

2 1 5 Leaf change

Tsanov (1984) conducted detailed phenological inventory on 38 species of willows Data are tabulated on dates for bud swelling flushing and leaf fall and the duration of growth which ranges from 198 to 282 days

Investigations carried out by Shimizu (1983) on a broad leaved evergreen forest revealed the presence of typical tropical characters associated with these forests These included long leaf flushing periods flowering and fruiting more than twice a year and large intraspecific variation

In the West African dry tropical forest in all species leaves were produced in synchronous flushes Flushing pattern varied between individuals within species although flushing activity was restricted to wet periods The restriction of leaf production to short synchronous flushes is adequately explained in terms of physiological constraints relating to avoidance of moisture stress Another possible reason may be escape from folivory (Lieberman and Lieberman 1984)

Booj and Ramakrishnan (1981) noted that most species in the montane forest of north east India produced new sprouts with the start of the warm period just before the rainy season Maximum leaf fall occurred during the dry winter months Fox (1972) noted that in north east Sabah many species produced a flush of new leaves with the start of very wet weather but leaf fall was more or less continuous and is especially heavy in drought periods Shedding may precede flushing or lag behind by a few days or weeks

2 1 6 Leaf litter falls

Leaf litter studies were conducted by Zohar (1984) on Eucalyptus camaldulensis in Israel He argued that spring leaf shedding appeared to be caused by atmospheric stresses brought on by low RH and high temperature The presence of strong winds may also have influenced the litter dynamics

Leaf fall occurs all the year round in tropical forests but peaks and troughs are not uncommon Bray and

Gorham (1964) studied the seasonal litter fall in the Colombian rain forests which showed a peak in March and least in July In evergreen seasonal forests the peak was usually during the first half of the dry season

2 2 Tree Architecture

2 2 1 Historical background

Studies on tree form so far have been the exception in tropical Botany as the main lines of this science accorded but little attention to structural characters only The study of the architecture and growth of tropical trees is a wide and almost a new field of research involving many different branches of botany such as descriptive and experimental morphogenesis phylogeny taxonomy and biogeography (Halle 1971)

The first synthesis works were published in 1970 (Halle and Oldeman) 1974 (Oldeman) and 1978 (Halle et al) They summed up and described the principal growth patterns of tropical trees and outlined the fundamental morphogenetic processes upon which tree architecture depends This procedure led to the recognition of some of the major growth processes which determine growth habits of tropical trees The discovery of the concept of the architectural model provided botanists with a powerful means of studying plant form Similar works were extended to lianas (Cremers 1973 1974 Huc 1975 Etifier 1981) grasses (Jeannoda 1977) and root structures (Kahn 1977) To date architectural analysis has amounted more than 150 families and certain groups (Blanc 1978 Castro e Santos 1981 Loup 1983 Temple 1977 Veillon 1976)

2 2 2 **Tree architectural studies Significance**

Tree architectural studies are a major contribution to the thriving discipline of plant ecology morphology and plant demography (Tomlinson 1987)

Moreover these works provided better insights into the constructional patterns of plants Some studies have already started to provide preliminary informations on the relationship between architecture and taxonomy (Kahn 1975) and between architecture and environment (Fournier 1979), on mechanisms of the hereditary transmission of form (Huc, 1977 Halle 1978) and on the analysis of reiterative processes and crown construction (Halle and Ng 1981 Torquebiau 1979)

2 2 3 **Tree growth**

Successful establishment of the seedling is obviously essential to the development of the tree and remains the most critical phase in the life cycle of a plant (Harper and White 1975) Of significance in the subsequent organization of the tree is the nature of the axis above the cotyledons Here a correlation between germination type and shoot organization is very evident (Halle <u>et</u> <u>al</u> 1978)

The existence of stages or phases in the development of individual woody plants has been documented Many trees as saplings show morphologically and physiologically distinct features which are either lost or change with age (Brink 1962 Moorby and Wareing 1963)

Tree shape is largely determined by its primary growth which reflects the environment of the time it grows (Esau 1965) Primary growth is initiated from an apical meristem while the cambium is responsible for the secondary growth (Whittaker, 1975 Waring and Schlesinger 1985)

Growth of the terminal shoot dictates a tree s architecture by controlling branch growth crown shape and stem growth Temperate and tropical trees grow in many patterns which may vary within and between species (Oliver and Larson, 1990)

Each year a tree s terminal and its lateral branches increase in length by adding new primary growth The year s growth from the terminal is referred to as leader or terminal shoot while the primary growths from the lateral branches are referred to as lateral shoots (Oliver and Larson 1990) Time of active elongation varies with climate species genotypes within species and local weather conditions (Zimmerman and Brown 1971)

In the architectural context a tree could be called as a population of meristems Meristems are the primary growth centres of the shoot system which by itself is a partly developed shoot (Romberger 1963) In architecture bud morphology is discussed in a dynamic context whose further development is conditioned by organized correlation within the whole tree

Halle et al (1978) recognised four major kinds of tree construction in meristematic terms for their description of architectural models (i) trees built by one meristem (ii) trees with modular construction (iii) trees with trunk branch differentiation (iv) trees with changes in orientation of axes

2 2 4 Definition

Architecture is defined as the visible but momentary expression of tree form and is based on the concept of architectural model an abstraction that refers to the genetically determined growth plan of the tree (Tomlinson 1987) The architecture of a plant depends on the nature and relative arrangement of each of its parts (Edelin 1990) The novel aspect of the architectural method compared with other morphological approaches is that it considers the plant as a whole however complex it is

2 2 5 Architectural model The growth characteristics

Tree architecture is the result of the activity of apical aerial and subterranean meristems (Halle 1971) So their structure sequence of differentiation through which they pass their longevity and rhythm of activity decides the architecture

Data on shoot morphology are very important In cocoa the spiral phyllotaxis of the trunk gives evidence of the radial structure of the meristem of this axis while the bilateral structure of the apical meristem of the lateral branches is clearly shown by distichous phyllotaxis (Greathouse and Laetsch 1969)

Monopodial and sympodial growth patterns forms fundamental distinction points in tree architecture and is dependent on the duration of activity of all meristems (Edelin 1990) However they are not exclusive and can be found on the same plant

Different kinds of meristems gives rise to axes with various biological and architectural properties A meristem with radial structure often produces an orthotropic and sexually sterile axis whilst a meristem with bilateral structure produces a plagiotropic axis which bears flowers (Halle, 1971)

Brink (1962) and Heslop Harrison (1967) noted that the structure of a meristem can become modified between the beginning and end of its life Such a change may take place wholly within the vegetative phase or involve a change from a vegetative to a reproductive phase Alternatively in the meristem there may be a change from a vegetative to a reproductive state and is reported to occur in the seedling meristem of Anthocleista nobilis G Don

The duration of the active life of the meristem is a very important factor determining tree architecture (Halle 1971) In Napoleana leonensis for example the seedling meristem was active throughout its entire life In some families the parenchymatous abortion of the meristem is a particular kind of differentiation which characterised their architecture (Prevost 1967)

The primary growth of an axis is the result of two coordinated, but distinct morphogenetic events, namely the organogenesis and elongation These events can take place rhythmically or continuously (Edelin 1990) In cocoa and mango the aerial meristems showed a characteristic alternation of rest and activity even in uniform climate which appeared to be regulated endogenously (Halle and Martin 1968) The architecture of the tree bears a mark of this rhythm

Tree crowns have precise construction (Halle and Oldeman 1970 1975 Halle et al 1978) So far 23 different tree architectural models have been recognized and named after prominent botanists on the basis of features of the gross branching system and not on conventional taxonomic criteria (Porter 1989)

2 2 5 1 Reiteration

Reiteration is a morphogenetic process through which the plant duplicates its own architecture totally or partially This has been called opportunistic behaviour by Halle et al (1978) The meristem behaves in such a way that the result is not a branch but a structure that is equivalent to a whole young tree (Oldeman 1990) Reiteration considered as the architectural expression of the equilibrium of a plant with its environment is of considerable importance for the plant (Edelin 1990)

The need to conduct phenological studies in different kinds of tropical environments is urgent Only through the analysis of intact ecosystems or communities may we hope to understand how these systems are organized biologically and how this organization has evolved Tree architectural studies helps in better understanding of the shoot growth rhythms of tropical trees The architectural approach to the analysis of plant form can also be used as a valuable descriptive device in systematics

Study Area and Methods

STUDY AREA AND METHODS

3 1 Study area

3 1 1 Location

The present study was carried out in Pattikad Range (between 76°15 and 72°27 E longitudes and 10°30 and 10° 2 N latitudes) in Trichur Forest Division

3 1 2 Climate

The area enjoys a warm humid climate having a mean annual rainfall of 2369 4 mm the bulk of which is received during the South West monsoon (Fig 1) Mean maximum temperature recorded at the nearby Kerala Forest Research Institute (5 km from the study area) ranges from 38 3°C to 29 6°C Mean minimum temperature varies from 23 9°C to 19 1°C

3 1 3 Physiography

The whole Forest Division has a highly rugged and undulating physiography wherein all kinds of aspects are met with

3 1 4 Geology, rock and soil

The active weathering of the ground is very much evident as indicated by the presence of boulders especially in

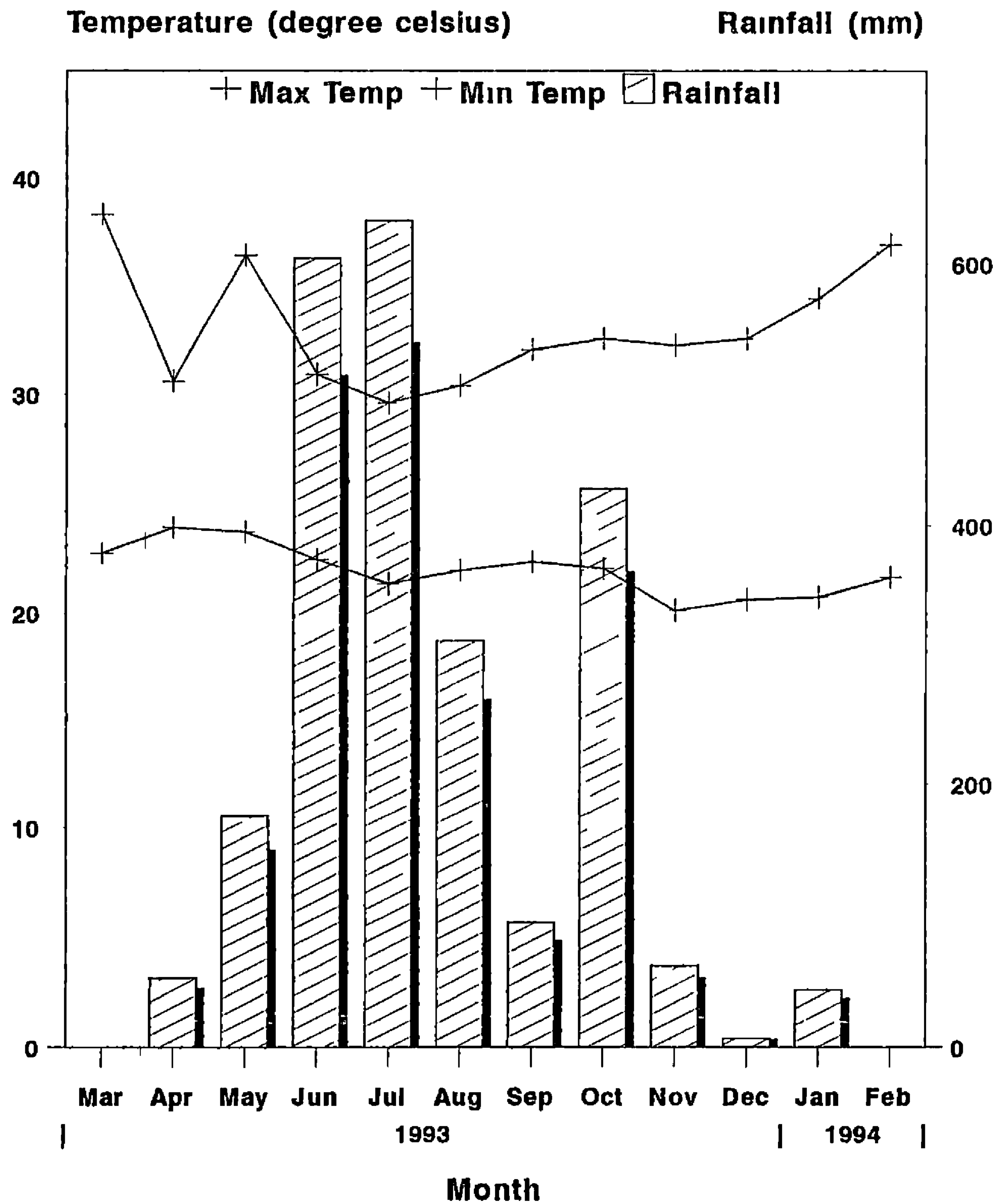


Fig.1 Weather Parameters for the Experimental Period (March 1993 to February 1994)

the moist deciduous tracts The predominant parent material seen is of metamorphic rocks of the gneiss series The soil is blackish or reddish and loamy

3 2 Methods

3 2 1 Choice of the tree species

Ten tree species each representing two forest types viz semi evergreen and moist deciduous tracts were identified for the pheno morphological study and tree architectural analysis They are

a Semi evergreen

1	*Aglai lawii* (Wt) Sald	Karakil
2	*Atalantia wightii* Tanaka	Kattunarakam
3	*Cynometra travancorica* Bedd	Koori
4	*Dimocarpus longan* Lour	Chempoovam
5	*Diospyros hirsuta* L f	
6	*Euodia lunu ankenda* (Gaertrn) Merr	Kanala
7	*Litsea stocksii* Hk f	Varicheera
8	*Memecylon molestum* (Cl) Cogn	Kanalei
9	*Persea macrantha* (Nees) Kosterm	Kulamavu
10	*Spondias pinnata* (L f) Kurz	Ambhazham

b Moist deciduous

1	*Dalbergia sissoides* Grah ex Wt & Arn	Eeti
2	*Dillenia pentagyna* Roxb	Vazhapunna
3	*Grewia tiliaefolia* Vahl	Chadachi
4	*Hollarhena pubescens* (Buch Ham) Wall ex Don	Kudagappala
5	*Lagerstroemia microcarpa* Wt	Venthekku
6	*Lannea coromandelica* (Houtt) Merr	Kalash
7	*Tectona grandis* L f	Thekku
8	*Terminalia paniculata* Roth	Pullamaruthu
9	*Terminalia tomentosa* var *crenulata* (Roth) Cl	Karimaruthu
10	*Xylia xylocarpa* (Roxb) Taub	Irul

3 2 2 Pheno-morphological studies

3 2 2 1 Site identification

A floristic survey was conducted in the study area to locate potential sites having a sizable population of all the above mentioned species Regular monthly visits were made to these sites for a full calender year starting from March 1993 to February 1994

3 2 2 2 Observations

During such visits the plants described were examined in detail with naked eyes and also by using binoculars

Attention was paid to the different types of phenological events like leaf shedding leaf renewal flowering and fruiting recording their developmental stages

Apart from these life cycle events the macro morphological features of the trees were also recorded Attention was paid to the type and arrangement of different kind of plant organs like inflorescence leaf and bark characteristics

3 2 3 Tree architecture and growth dynamics

A number of individuals of each of the chosen species of different ages were subjected to observation of five groups of characteristics that largely determine the structure of the plant following Edelin (1990)

The five groups of characteristics are

a Monopodial or sympodial growth

In a monopodial system meristem growth is practically indeterminate while in a sympodial system each meristem has short or middle term determinate growth

b Rhythmic or continuous growth

The growth is rhythmic when there is a regular alternation of elongation and resting periods Continuous growth is characterised by the total absence of a resting period

c Aerial vegetative branching pattern

Branching can be either terminal or lateral

d Orthotropy and plagiotropy

An axis is orthotropic when its growth direction is vertical On the contrary a plagiotropic axis develops on a horizontal plane

e Position of sexuality

Sexuality can be terminal or lateral

Using these observations the specific structural pattern for each species was observed and the totality of events marking their development were defined

Results

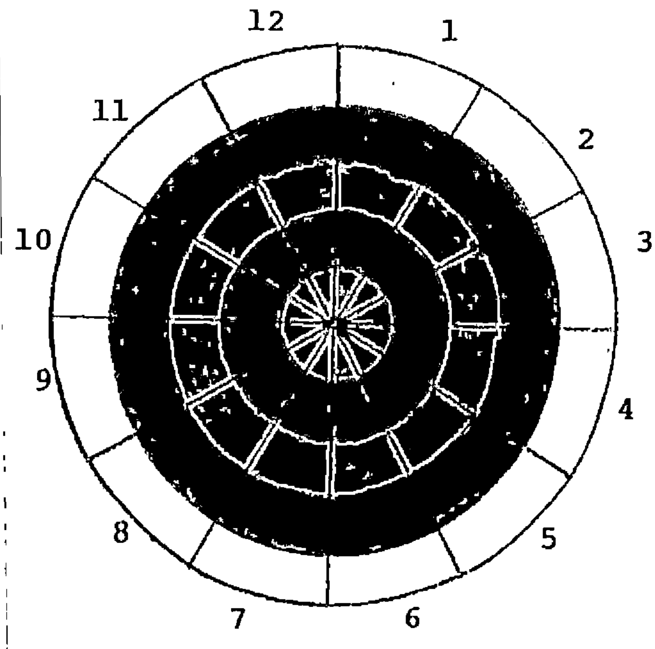
RESULTS

Results of the study conducted to gain more information on the phenology and macro-morphological features of selected tree species are outlined below.

4.1 Phenology and macro-morphology

4.1.1 Phenograms

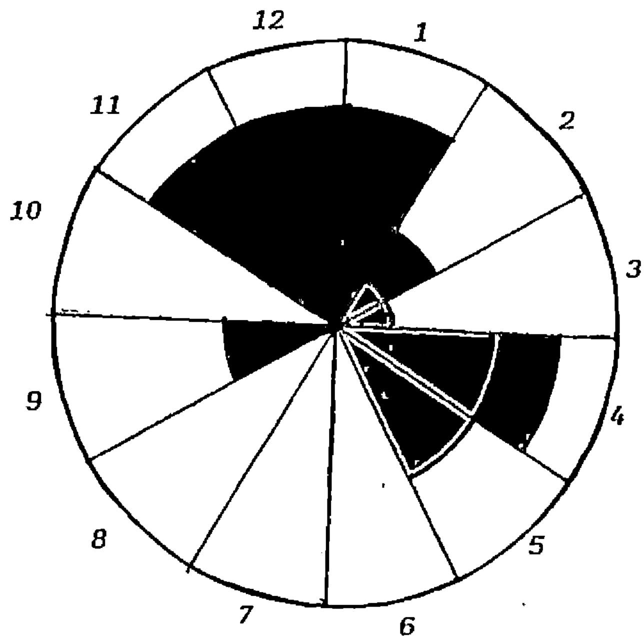
The recorded observations in phenology of 10 deciduous and 10 semi-evergreen species are presented in the phenograms. Each phenogram describes the phenological calendar for a species. Apart from the seasonal phenological phases, important macro-morphological features of each of the species are also listed along with.



A - Leaf fall
B - Flowering
C - Flushing
D - Fruiting

Nos.1-12 in circle represent months in an year

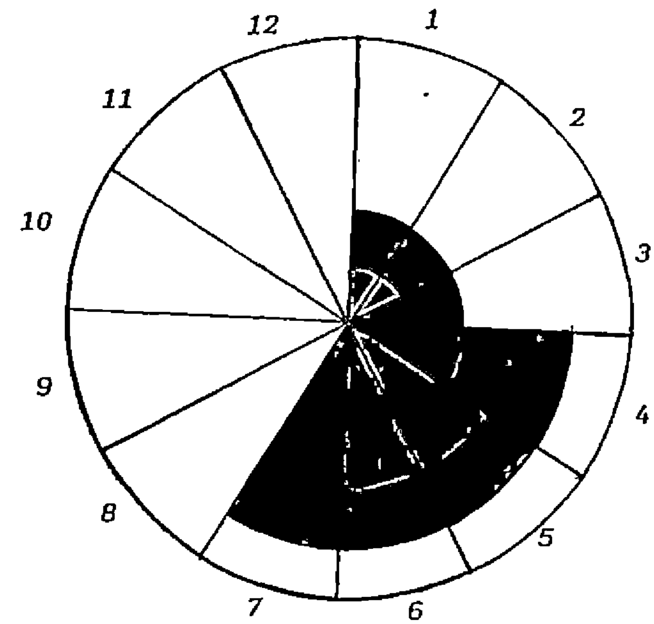
LEGEND OF THE PHENOGRAM
(Moist deciduous flora)



<u>Dalbergia</u> <u>sissoides</u> **Grah. ex. Wt. & Arn.** **Fabaceae**

Large deciduous (nearly evergreen) tree with a serpentine trunk and having full rounded crown. Compound leaves, the leaflets being orbicular and obtuse or emarginate. Compound leaves are arranged alternately, the lateral leaflet being smaller than the terminal one. Flowers are pure white, arranged in panicles. Fruits are flat, indehiscent pods. Bark fairly thin and brownish grey.

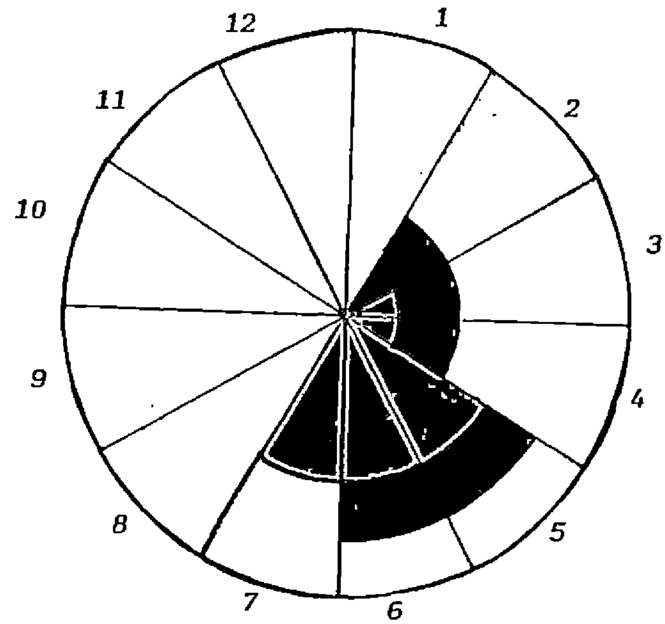
Leaf shedding about February to March. New leaves started appearing in April-May. Flowers appeared mainly in January-February, but few individuals did flower in September also. Fruiting extended over a period from November to April.



<u>Dillenia</u> <u>pentagyna</u> Roxb. Dilleniaceae

A large deciduous tree with a rounded crown and very large leaves. Leaves silky pubsescent when young. Large dentate or crenate leaves are crowded at the ends of thick branchlets in trees. Bark greyish brown, smooth with shallow depressions. Flowers yellow coloured and borne in fascicles. Fruits yellow coloured, succulent and edible.

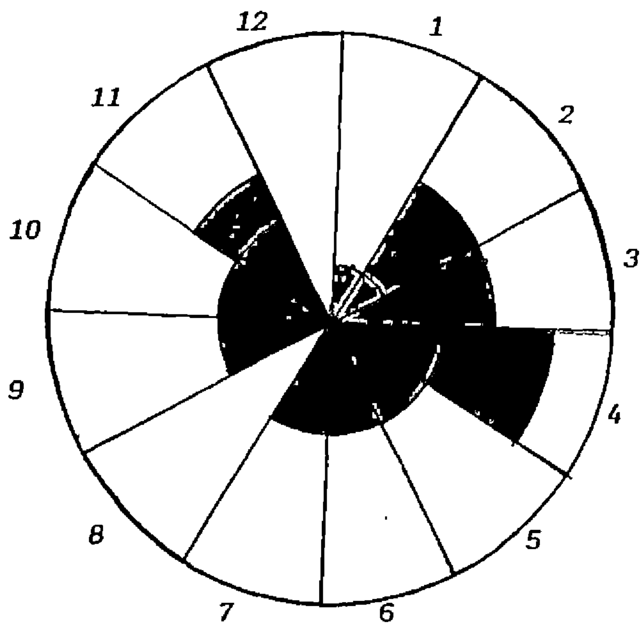
Leaves turned brown and fell during January-February. Flower buds also appeared during the same period. New flushes appeared with the start of the rains in May-June. Fruits ripened about April-July.



<u>Grewia</u> <u>tiliaefolia</u> Vahl. Tiliaceae

A medium sized deciduous tree with an irregular trunk. Leaves suborbicular and acute at apex. Alternate phyllotaxy. Flowers are yellow coloured and borne in clustered cymes. Fruit is a drupe. Bark pale yellow to brown.

The tree sheds its leaves from March to April. Flowers starts appearing from February to April. Sprouting commences before the onset of monsoon in May and is extended upto July. Fruits can be seen on the trees in May and June.



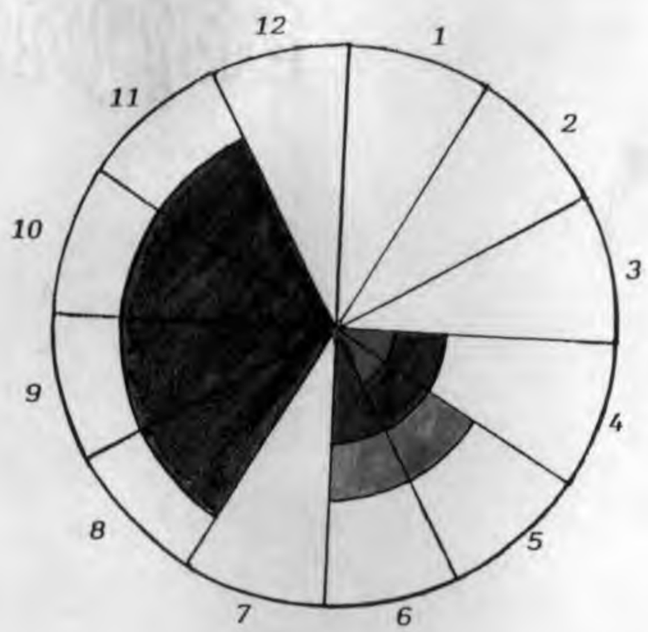
<u>Holarrhena</u> <u>pubescens</u> (Buch.-Ham.) Wall. ex Don   Apocynaceae

A small or middle sized deciduous tree with opposite, entire leaves. Young shoots sometimes tomentose. Flowers are whitish, fragrant and are arranged in terminal corymbose cymes. Fruits are pairs of slender follicles. Bark greyish brown and scaly.

Leaf fall was noticed during January-February. Two flowering cycles i.e., one from April-July and the second starting from September-November were recorded. New leaves appeared about March, but in some individuals flushing could be seen again in November. Fruits appeared by April.

Plate I   Hollarhena pubescens branch with white flowers

Plate II   An adult Lagerstroemia microcarpa bare of foliage. Note the smooth, pale bark and the orthotropic branches

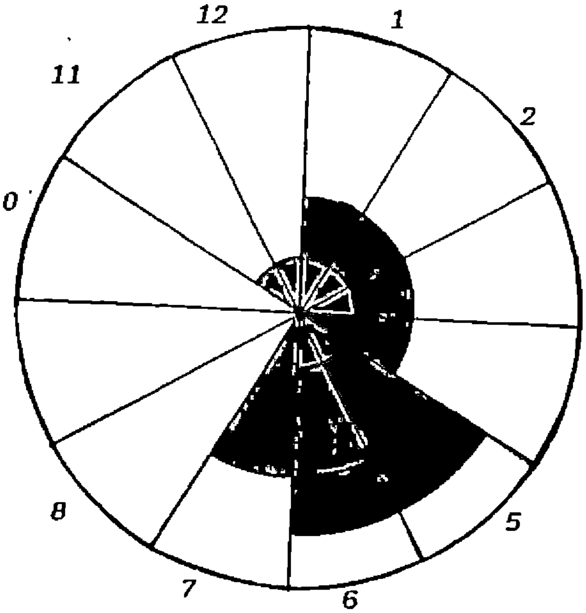


Lagerstroemia microcarpa Wt. Lythraceae

Large deciduous tree. Leaves alternate, glabrous, secondary nerves prominent and arching. Flowers borne in large terminal panicles. Bark smooth, pale, exfoliating in large papery strips.

The leaves started falling by April-May. Flowers started appearing from April itself. New leaves started appearing before the onset of rains in end May and was continuous in the rains. Fruiting period extended from August to November.

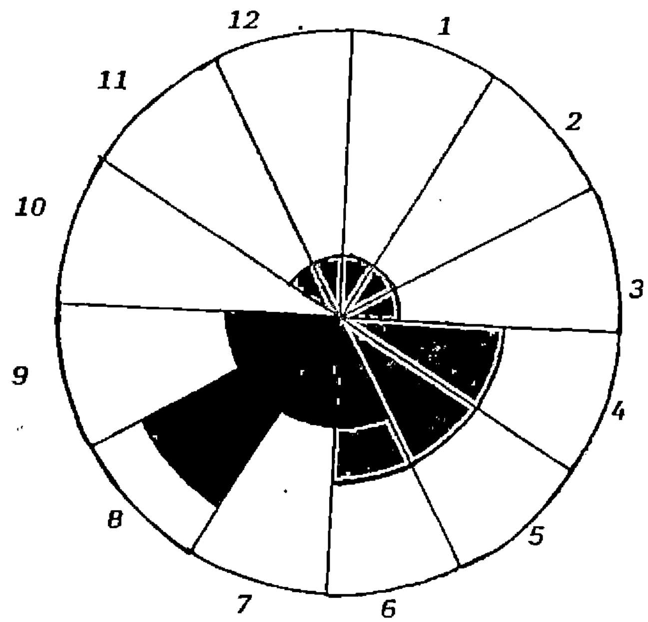
Plate III Pitch black bark of Lannea coromandelica



<u>Lannea</u> <u>coromandelica</u> (Houtt.) Merr. Anacardiaceae

Large sized deciduous tree with a spreading crown. Leaves are large, compound and inparipinnate. Leaflets are opposite and entire. Flowers are feathery white blossoms borne in stiff terminal racemes. Fruit is a drupe. Bark pitch black to grey and smooth.

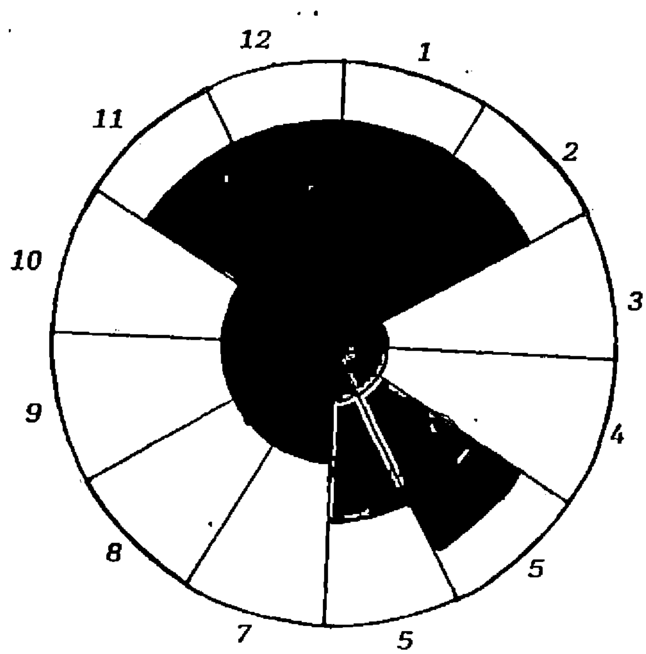
Leaf fall extended over a longer period i.e. from November to March and again from May to June. Flowers appeared when the tree was leafless. New sprouts appeared during the rains in July. Fruit appeared rapidly around May-June.



<u>Tectona</u> <u>grandis</u> L.f. Verbenaceae

Large deciduous tree with a rounded crown and a tall clean cylindrical bole. Branchlets quadrangular and channeled. Leaves simple, opposite, large, broadly elliptical or obovate, rough above. Flowers white, borne in erect terminal panicles. Fruit is a hard, bony nut. Bark greyish brown.

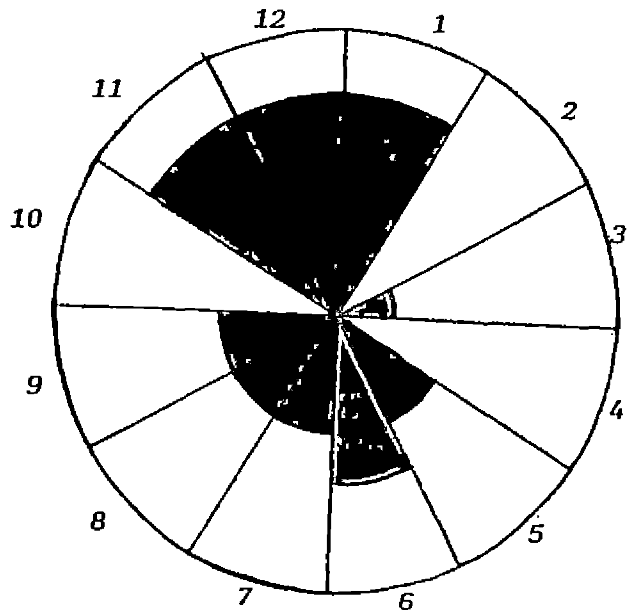
Leaf shedding started from November and is extended upto March. Flowering was during the rainy season i.e, June to September. New leaves started appearing by April. Fruits ripened on August.



Terminalia paniculata Roth   Combretaceae

A large to very large deciduous tree. Leaves glabrous, oblong. Upper leaves alternate while the lower ones are opposite. Lower part of the bole is often fluted. Flowers are small, whitish in rusty panicled spikes. Fruits, brick red with one large wing and two smaller wings. Bark dark brown, rough with shallow longitudinal and transverse fissures.

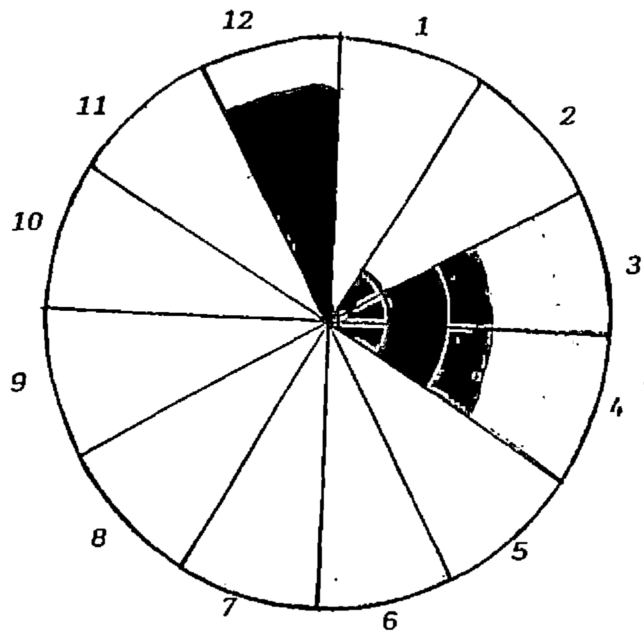
The leaves were shed during March-June. Flowers could be seen for half of the year from July to December. New sprouts appeared by May-June. Fruits ripened from November to February.



<u>Terminalia</u> <u>tomentosa</u> var. <u>crenulata</u> (Roth) Cl. Combretaceae

Large deciduous tree with a long clean bole and a full crown. Leaves simple, exstipulate, alternate. Two small glands present near the base of the lamina on under surface. Young seedlings have a characteristic bend at the collar region. Whitish blossoms, in panicled spikes. Fruit has a hard bony axis with five coriaceous wings. Bark, with typical deep longitudinal fissures and transverse cracks, is grey to black in colour.

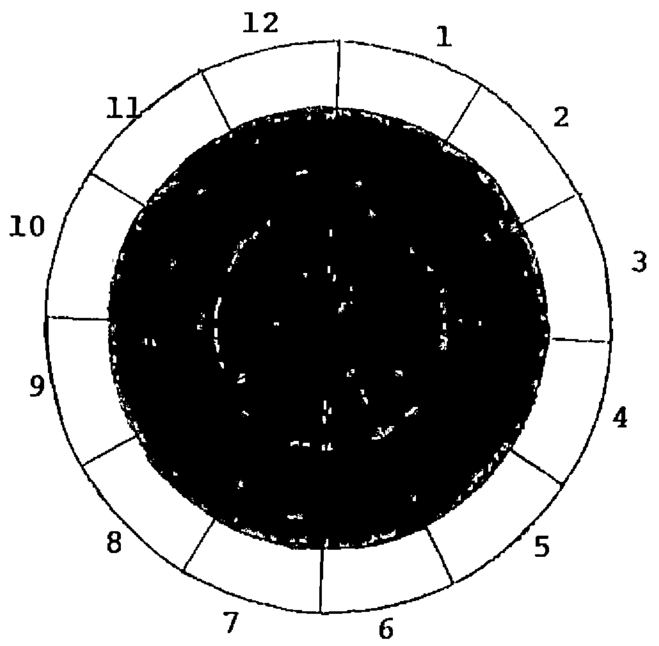
Leaf shedding by March. Flowers started appearing with the rains and was extended upto September. New leaves also appeared in June. Fruiting commenced later from November-January.



<u>Xylia</u> <u>xylocarpa</u> (Roxb.) Taub Mimosaceae

A large sized deciduous tree. Young parts pubescent. Leaves bipinnately compound. Reddish brown glands could be seen on the rachis. The globose fragrant flower heads are yellowish white in colour. Pods are brown and woody. Bark smooth reddish grey, exfoliating in irregular flakes.

The leaves commence falling by February. Flowers also appeared about the same period. The new leaves appeared in March-April. Fruits appeared late in the year.



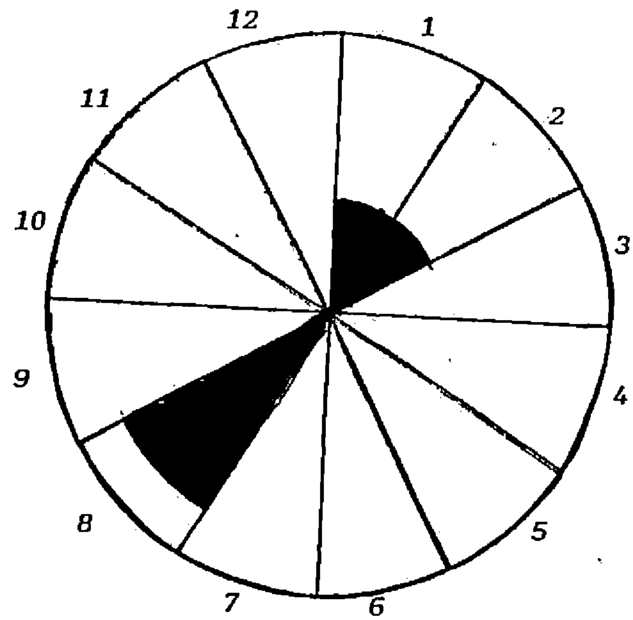
A - Flowering

B - Fruiting

Nos. 1-12 in cricle represent months in an year

LEGEND OF THE PHENOGRAM

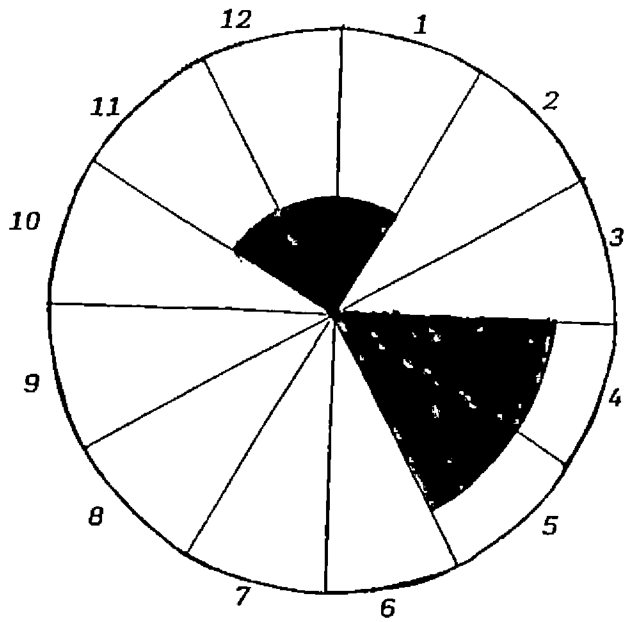
(Semi-evergreen flora)



<u>Aglaia</u> <u>lawii</u> (Wt.) Sald Meliaceae

A small sized semi-evergreen tree. Leaves imparipinnate, leaflets entire acute or acuminate. Alternate phyllotaxy. Fruit is capsule. Bark greyish brown. Flowers borne in panicles.

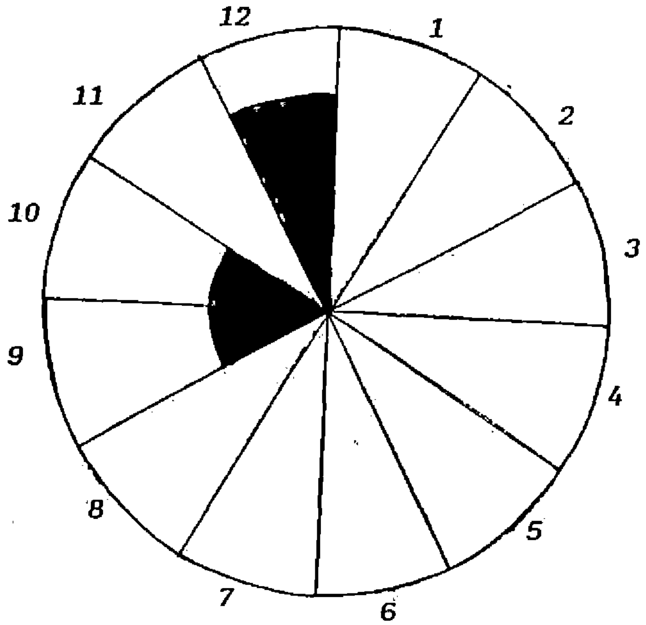
The flowering season was January-February. Mature fruits were borne in August.



<u>Atalantia</u> <u>wightii</u> Tanaka — Rutaceae

A small armed evergreen tree. Leaves elliptic or ovate lanceolate, acute, entire, glabrous and olive green in colour. White flowers are borne in short axillary, corymbose cyme. Fruit is a berry. Bark is dull brown in colour.

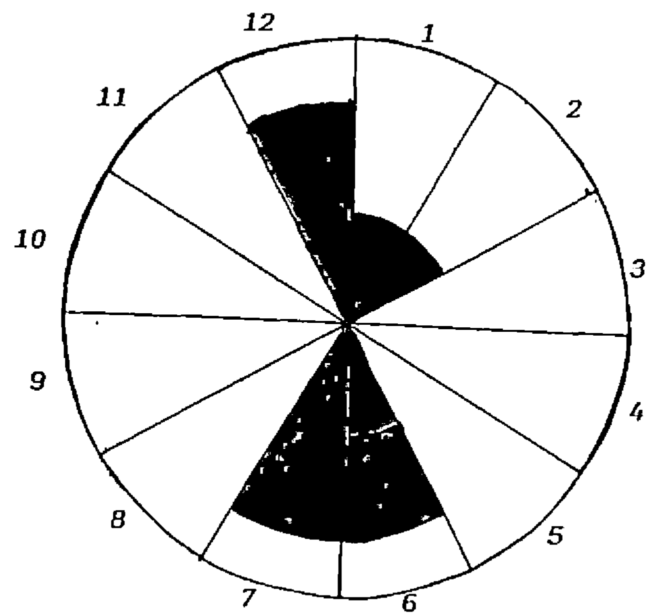
Flowering period of this tree was from November to January. Fruits were produced during April-May.



Cynometra travancorica Bedd Caesalpiniaceae

A medium sized evergreen tree. Young shoots are creamy pink. Leaflets one pair, unequal sided, almost falctate. Rosy white flowers are borne in compact short axillary cymes. Pods are flat. Bark pale yellow to dull grey with a smooth texture.

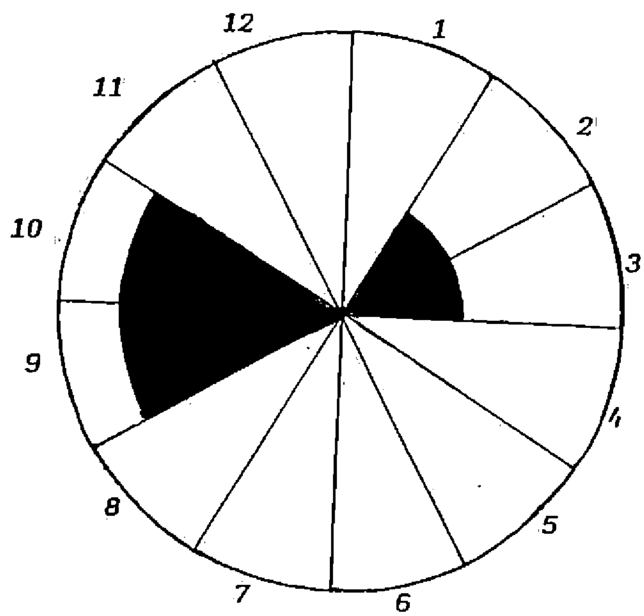
Flowers started appearing in September-October. Fruits matured later in the year in December.



Dimocarpus longan Lour. Sapindaceae

A middle sized tree. Leaflets coriaceous, two to five pair, shining above, glaucous and often slightly pubescent beneath. Young leaves bright red, acuminate and glabrous. Yellowish white flowers are borne in terminal panicles. Fruit globose and reddish in colour. Bark is brownish grey in colour and rough.

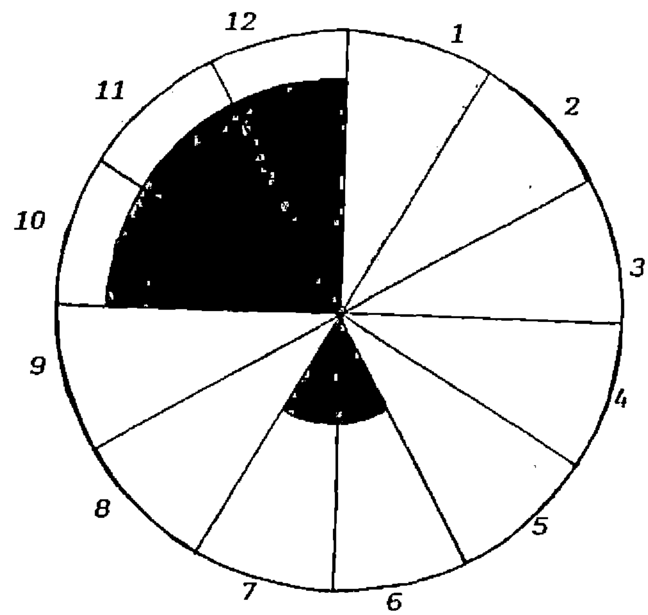
Flowers appeared during January-February and again in June. Fruiting was in June-July and during December.



<u>Diospyros</u> <u>hirsuta</u> L.f. Ebenaceae

A small sized evergreen tree. Leaves entire acuminate and tomentose beneath. Flowers are brown in colour and fascicled. Fruit globose and green. Bark black and dark grey.

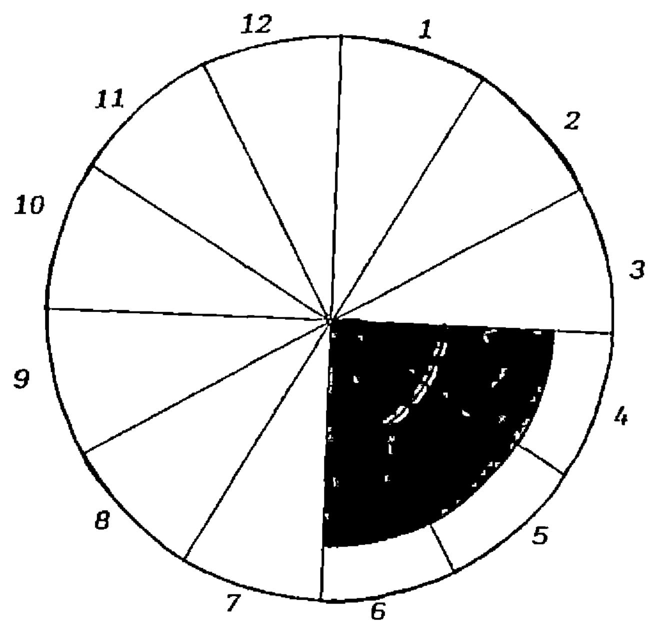
Flowering was initiated from February-March. Fruits started appearing by September-October.



Euodia lunu-ankenda (Gaertn.) Merr. Rutaceae

A small to medium sized tree with opposite branches. Young shoots pubescent. Leaves trifoliate, leaflets entire, acute and glabrous. Greenish white flowers are borne in axillary panicled cymes. Seeds are black. Bark is smooth and grey.

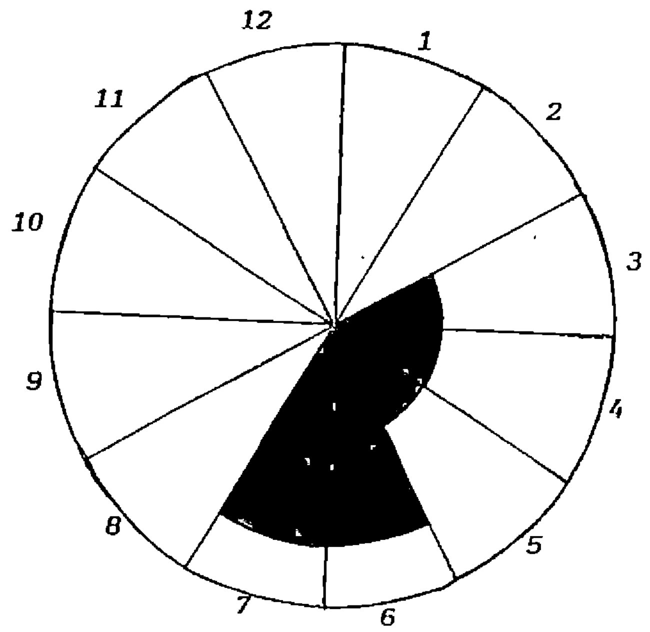
Flowering was on June-July while fruits started appearing from October to December.



Litsea stocksii Hk.f. Lauraceae

A small sized tree, glabrous except the brown velvety inflorescence and very minute hairs occasionally on the underside of the leaves. Leaves are coriaceous and glaucous beneath. Flowers are borne in racemes. Fruit is an ellipsoid berry. Bark smooth.

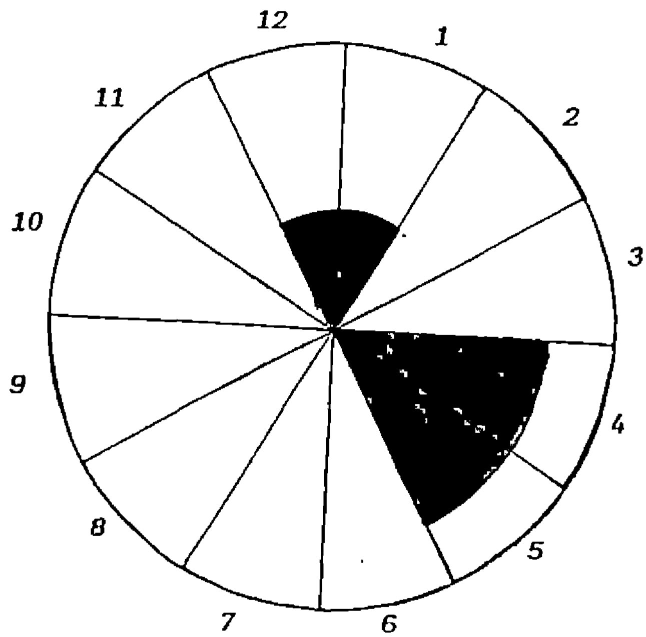
Flowering started around April and was extended upto June. Fruits appeared simultaneously from April to June.



Memecylon molestum (Cl.) Cogn. Melastomataceae

A small evergreen tree with brilliant blue flowers. Leaves glabrous, yellowish-green and sub-sersile. The blue flowers are borne in axillary, laterally branched cymes. Fruit is a black purple, globose berry. Bark light brown and rough.

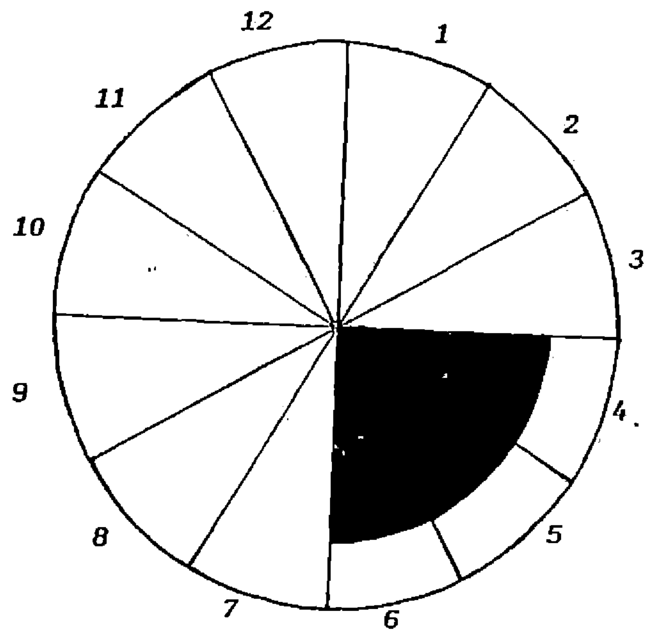
Flowers started appearing from March to May. Fruiting was initiated by June and could be seen during July also.



Persea macrantha (Nees) Kosterm. Lauraceae

A large evergreen tree with glabrous leaves alternately arranged. Leaves can be seen close together at the tips of twigs. Young flushes are reddish yellow. Yellowish flowers are borne in panicles. Fruit is a round black berry. Bark pale brown.

Flowers were borne in December-January. Fruits appeared in April-May.



Spondias pinnata (L.f.) Kurz. Anacardiaceae

A large sized semi-evergreen tree. The leaves are compound, inparipinnate and fragrant. Inflorescence consists of whitish flowers. Fruits are pendulous clusters of drupe. Drupe yellow when ripe. Bark aromatic and is smooth grey in colour.

Flowering and fruiting were simultaneous phenomena initiated from April upto June.

4.1.2 Observed seasonality

4.1.2.1 Moist deciduous species

Data collected on the patterning of the seasonal events observed for a calendar year are presented in Table 1.

4.1.2.1.1 Leaf fall pattern

The moist deciduous species shed their leaves during the period from February to May (Fig.2). In March, Maximum number of species (7) shed their leaves, followed by February (4), April (4) and May (3). No leaf fall was observed during the months of July, August, September and October. Only one species shed its leaves in June.

4.1.2.1.2 Flowering pattern

The phenomenon of flowering in the same set of species, too was confined to the early part of an year (Fig.3). Maximum number of species (6) bloomed during April, while in February, March, July and September, four out of the ten species were observed to flower. In January, June and August, three species bore flowers, while during May, October and November it was only two. However, flowering was observed to be occurring throughout the year, with the least occurrence being recorded in December. Only one out of the ten species was observed to blossom during that month.

Table 1. Number of species which exhibited the stated phenological behaviours in the moist deciduous forest for a calender year

Months	Number of species			
	Flowering	Fruiting	Leaf fall	Flushing
March	4	1	7	2
April	6	5	4	1
May	2	5	3	4
June	3	7	1	3
July	4	4	0	0
August	3	0	0	2
September	4	0	0	1
October	2	0	0	1
November	2	0	2	5
December	1	0	2	4
January	3	0	2	3
February	4	0	4	3

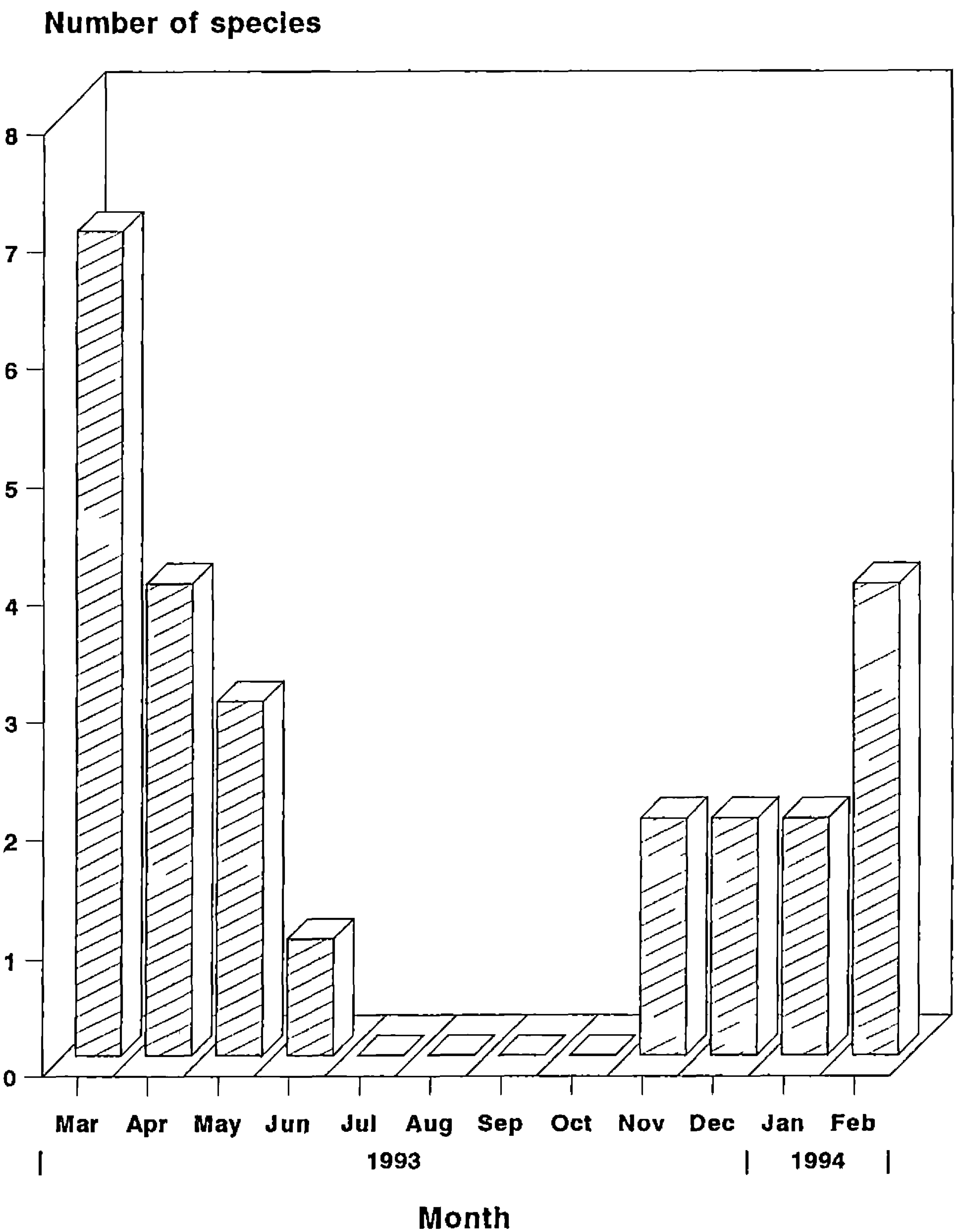


Fig. 2 Number of species which exhibited leaf fall

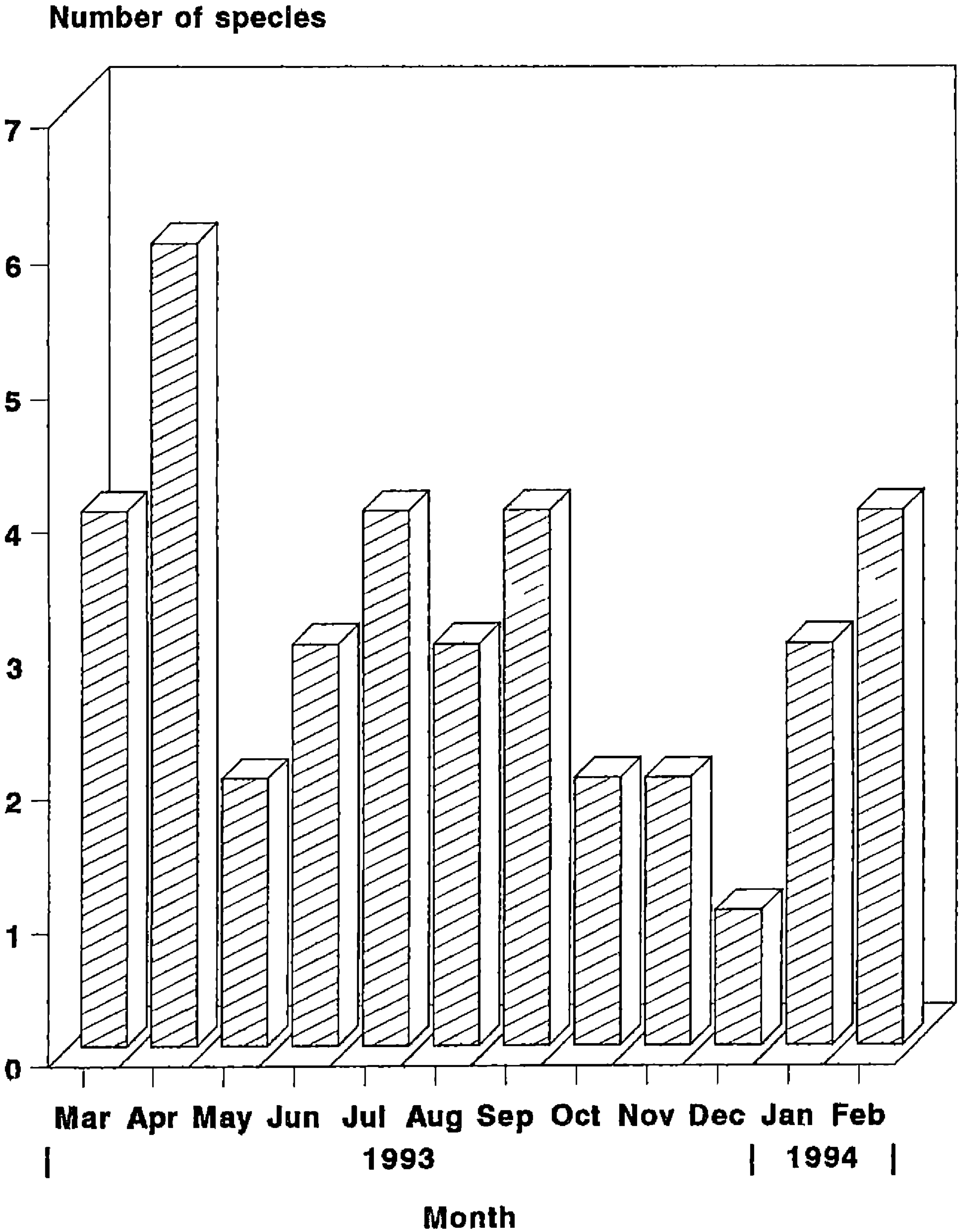


Fig. 3 Number of species which exhibited flowering

4 1 2 1 3 Flushing pattern

Coming to the phenomenon of leaf renewal sprouts emerged profusely from the month of November onwards (Fig 4) Half of the total species observed were found to initiate flushing during this period The number of species producing flushes declined progressively during December (4) January (3) February (3) and March (2) However by May after a brief lull in April (1) four species were observed with sprouts During September and October the number of species exhibiting flushing was limited to one But no new growth was observed during the month of July

4 1 2 1 4 Fruiting pattern

The fruiting pattern of the moist deciduous species revealed a peculiar seasonality (Fig 5) The species produced fruits only during the months of March April May June and July No fruiting was observed from August to February Heavy fruiting was recorded during June when seven of total ten species bore fruits The months of April and May also were good fruiting months (5) But fruiting was very low in the month of March (1)

4 1 2 2 Semi evergreen species

Data on the phenological behaviour of the semi evergreen species are presented in Table 2

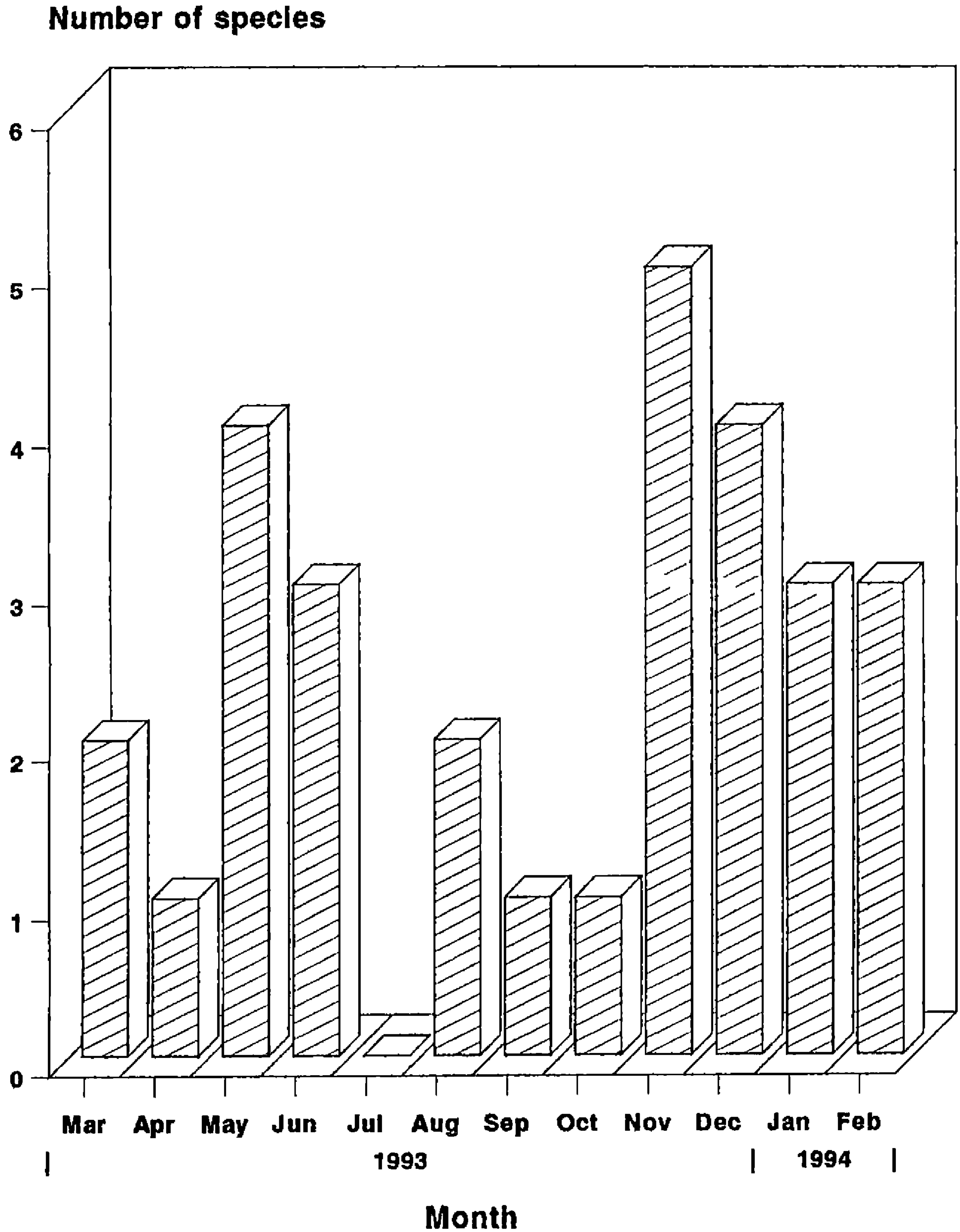


Fig. 4 Number of species which exhibited flushing

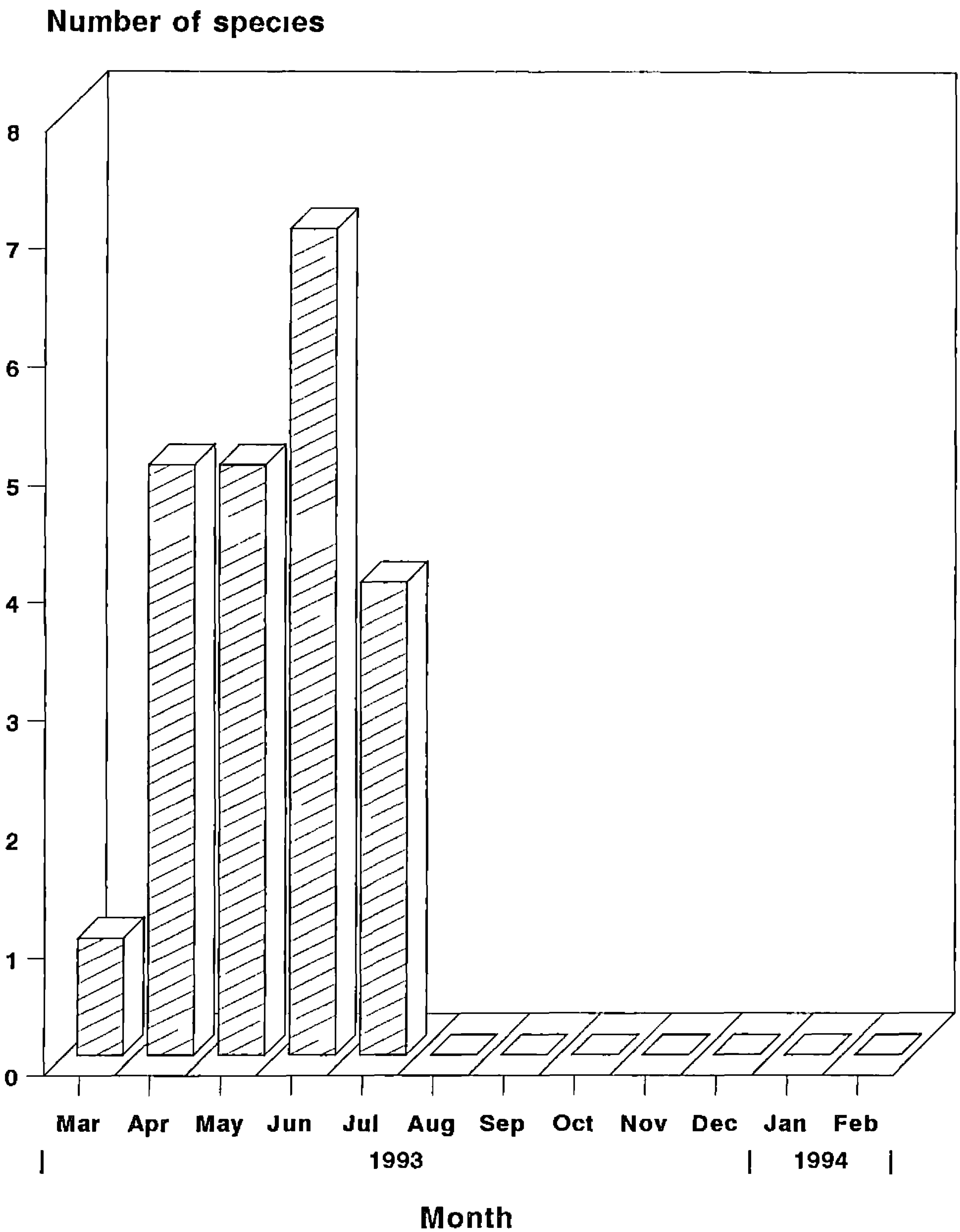


Fig. 5 Number of species which exhibited fruiting

Table 2 Number of species which exhibited the stated phenological behaviours in the semi evergreen forest for a calender year

Months	Number of species	
	Flowering	Fruiting
March	2	0
April	3	4
May	2	4
June	4	4
July	1	2
August	0	1
September	1	1
October	1	2
November	1	1
December	2	3
January	4	0
February	3	0

4 1 2 2 1 Flowering pattern

Two flowering peaks were observed during the month of January and June (Fig 6) Maximum number of species (4) flowered during these two months Flowering was also high during the months of April and February (3) In the months of March May and December two out of the ten species were in blossom Flowering was low (1) during the months of July September October and November However no species flowered during August

4 1 2 2 2 Fruiting pattern

Fruiting peaked during the months of April May and June (Fig 7) Out of the total ten four species bore fruits during these months In December also three species were seen with fruits Two species had fruits in July and October while in August September and November fruiting was low (1) The months of January February and March were observed to be fruit free periods

4 2 Growth dynamics

4 2 1 Moist deciduous species

4 2 1 1 *Dalbergia sissoides*

When young *Dalbergia sissoides* has an orthotropic monopodial trunk with rhythmic growth Phyllotaxy is

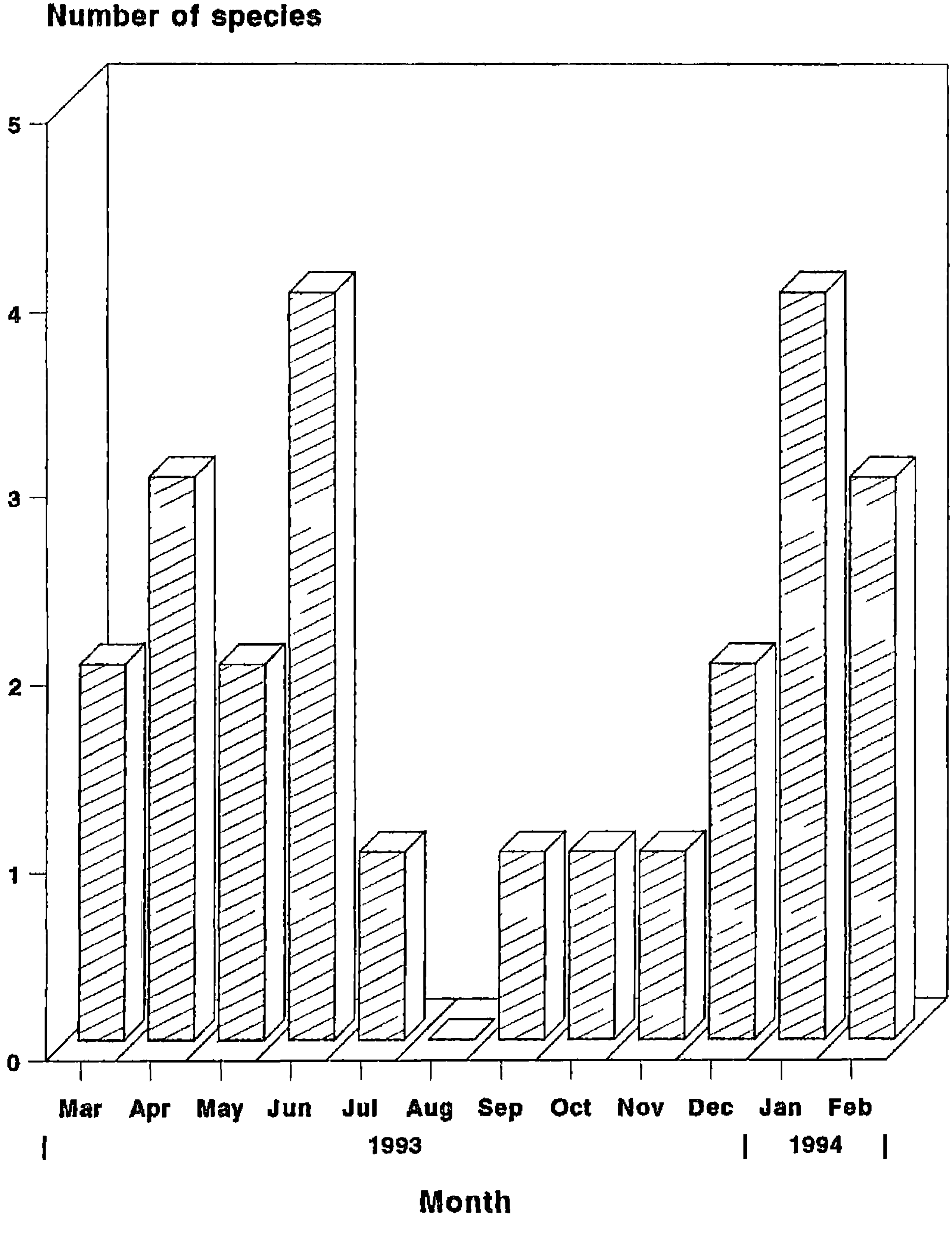


Fig. 6 Number of species which exhibited flowering (semi-evergreen)

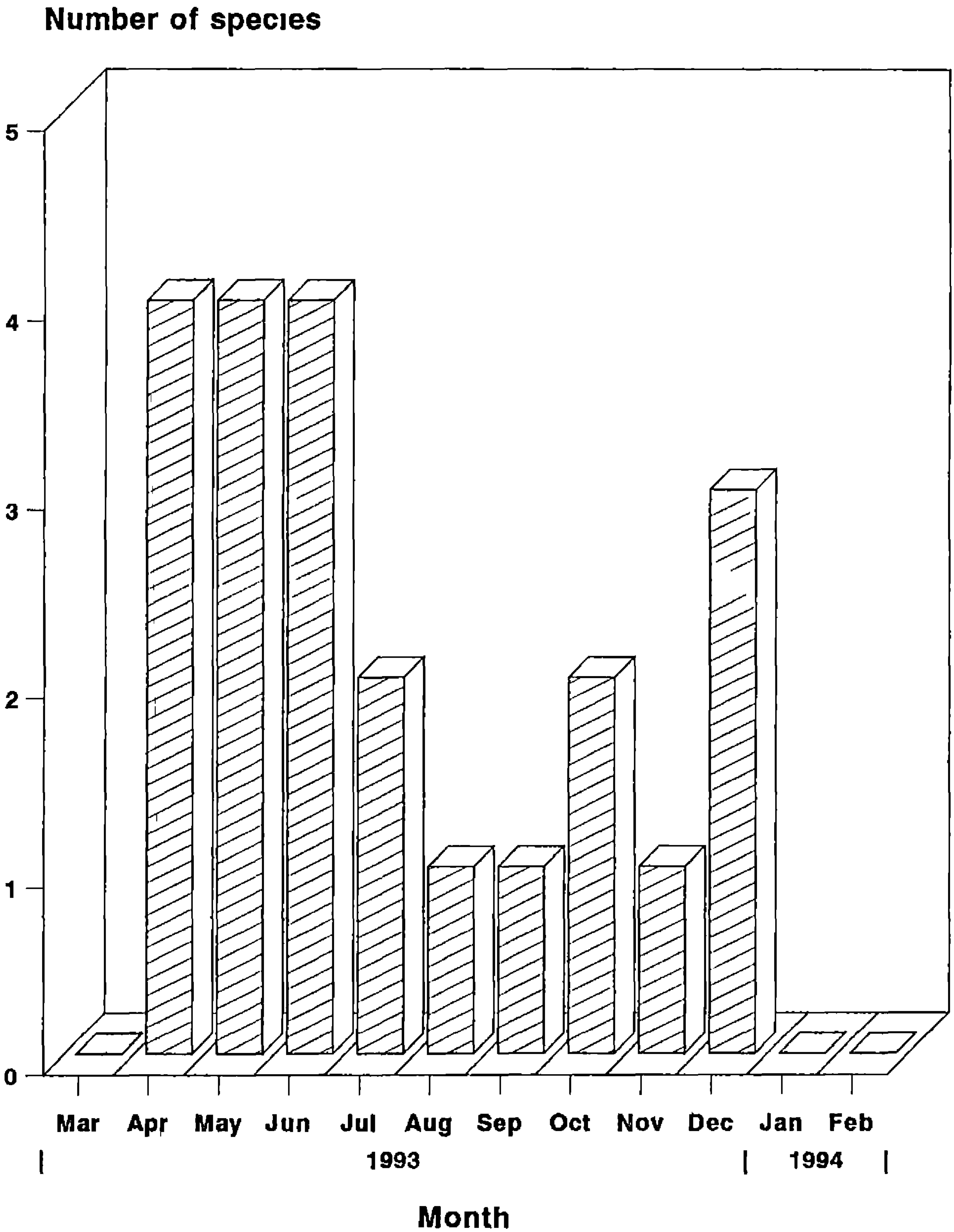


Fig. 7 Number of species which exhibited fruiting (semi-evergreen)

alternate the leaves stipulate and imparipinnate The branches are sympodial and orthotropic These branches which produces the compound leaves are produced alternately The leaf axils on the branches itself are orthotropic In young trees leaves are either borne directly on the lateral extension from the branches or directly from the branch Although a lateral branch system is initiated as a single entity, it could be seen that such a system consist of numerous sympodial units ie within a single axis a series of aborted buds could be located in the branch axils

Leaves are mostly confined to the periphery of the branch axis the sympodial nature of the branch could be clearly seen highlighted by the scars left over by the aborted buds Another typical feature of this species is that both the main and the lateral axis have a characteristic S shaped curling which vanishes as age advances

4 2 1 2 <u>Dillenia pentagyna</u>

The seedlings of Dillenia possesses an orthotropic straight stem At very young stage contracted scars of leaves and axillary buds could be noticed in the nodes Phyllotaxy is spiral the leaves are typically bundled at the top of the stem Leaves are exstipulate simple and petiolate The rosette like leaf arrangement of the species is peculiar The petiole base is often winged and initially protects the terminal bud subsequently it protects the axillant lateral bud

In the moist deciduous tracts the main axis assumes a heavily branched sympodial nature The lateral axes are all orthotropic The branches bears scars seems to be left by the cadaucous leaves While the terminal bud at the end of the rosette expands the leaves fall off subsequently elongating the branch or main axis

4 2 1 3 Grewia tiliaefolia

The seedling of Grewia bears oblique leaves inserted on the axis with alternate phyllotaxy Large leafy stipules is a distinguishing feature

The juvenile tree has an orthotropic trunk meristem with continuous growth Continuous branching is the rule The orthotropic axis produce branches but in no distinct pattern The branches have a characteristic ziz zag nature and are more or less plagiotropic Branches themselves did exhibit different levels of plagiotrophy in different individuals Pronounced leaf dimorphism is encountered towards the tip of the branches the leaves are larger in size

Plate IV Young Dillenia with large leaves arranged typically towards the branch apexes

Plate V The quadrangular orthotropic monopodial trunk of a young Teak tree bearing opposite plagiotropic branches Scars of old scale leaves shows off its rhythmic growth nature

4 2 1 4 Holarrhena pubescens

The species has an orthotropic trunk with a large number of orthotropic lateral units Phyllotaxis is opposite

The main trunk axis is a sympodium The scars seen on the main trunk highlights the rhythmic growth of the sympodial unit The lateral axes too bear these scars Sexuality is lateral All the axes are orthotropic

From the seedling stage to that of the adult tree the axes undergo a sequence of developmental patterns Young seedling have a sympodial orthotropic main axis on which subsequent orthotropic branch tiers are inserted Flowering does not arrest the development of a lateral axis and vegetative growth from the same end is continued

4 2 1 5 Lagerstroemia microcarpa

The young Lagerstroemia seedling has an erect orthotropic axis As the species mature orthotropic branch axes are initiated However it is quite evident that the lower order branches tend towards a plagiotropic condition unlike the higher order branches which are strictly orthotropic Leaves are arranged sometimes alternatively but opposite phyllotaxis is the rule Sexuality is terminal and determinates the vegetative growth of the bearing axis

The leaves are borne in a pendulous nature in the orthotropic branches Branches consist of numerous sympodial units Overall the growth of the species is in a rhythmic manner

4 2 1 6 *Lannea coromandelica*

The tree is deciduous with stout soft branches Main orthotropic trunk axis has lateral orthotropic branch axes which are sympodial Growth is rhythmic Phyllotaxy is alternate

4 2 1 7 *Tectona grandis*

Teak follows a rhythmic growth pattern which consists of two consecutive growth phases At juvenile stage the tree is monopodial Numerous plagiotropic to orthotropic branches are produced on the orthotropic trunk Flowering terminal on every axis brings an end to this schematic growth A sympodial development with determinate modules having terminal inflorescence is initiated More and more reiterated complexes grow on the limbs which reproduce terminally and die out Continuous replacement of these complexes ensures the development of the tree

4 2 1 8 *Terminalia paniculata*

The tree has a monopodial trunk with rhythmic growth and decussate phyllotaxis bearing branch tiers with similar phyllotaxis Branch growth also in rhythmic and each branch plagiotropic by apposition

The seedling axis is orthotropic and growth rhythmically each flush separated by a series of close set leaf scars Eventually a pattern of monopodial branching is initiated In the leaf axils dormant and live buds could be seen

Sexuality is terminal and vegetative growth of the branches are indeterminate At a distal view all branches seem to droop while the tips are always positively phototropic

4 2 1 9 Terminalia tomentosa var crenulata

This tree also follows the same developmental pattern as that of Terminalia paniculata

Seedling starts its life on a monopodial orthotropic trunk with a rhythmic growth pattern Phyllotaxy is opposite A monopodial branching pattern is initiated and each branch is plagiotropy by apposition

At the base of each branch a pair of small leaves can be found which could be taken as an indication of a newly formed branch Branches are also noted to arise from the axils of leaves In younger trees there is a progressive downward bending of the individual branches as they age Sexuality is terminal

4 2 1 10 <u>Xylia</u> <u>xylocarpa</u>

The seedling axis of Xylia is an orthotropic axis with rhythmic growth Leaves are arranged in spiral phyllotaxis Leaf dimorphism is evident, the terminal leaflets are larger

Strictly orthotropic branches are later formed on the main trunk In older individuals branches are mostly confined to the upper storey while one or two small ones could be seen in the downmost stratum Glands can be seen on the axil of every leaf

4 2 2 Semi-evergreen species

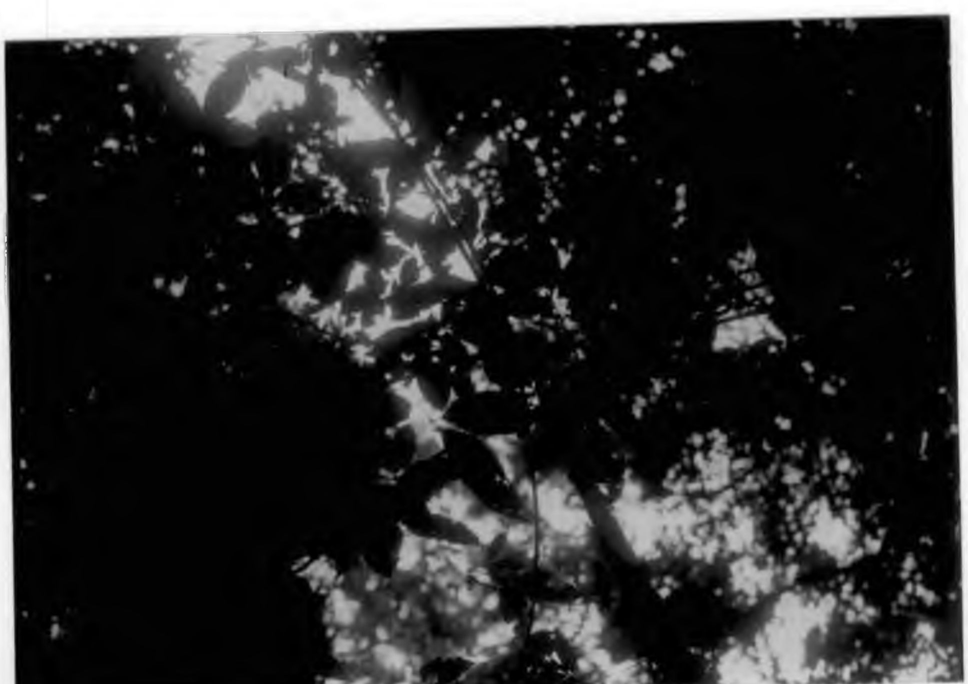
Results of the observations on the growth dynamics of the semi evergreen species are presented below It may be noted that the observation of standing trees in a evergreen tract coupled with the tree s structural complexity limits a detailed analysis of the principles of construction

4 2 2 1 <u>Aglai</u> <u>lawii</u>

The tree has an orthotropic trunk with alternate compound leaves The young parts especially the leaves and

Plate VI _Terminalia_ _tomentosa_ Var _crenulata_ seedling with its highly orthotropic growing axis

Plate VII A young Euodia tree Note the branch axes arrangement



the branchlets are pubescent The leaves have an indeterminate growth as a result of the activity of an apical bud Older leaflets are lost during this time

Branches are orthotropic having a rhythmic growth pattern

4 2 2 2 Atalantia wightii

The tree has axes differentiated into trunk and branches armed with spines The trunk is orthotropic with profuse branching Underdeveloped leaf buds are represented by stipule like scales Branches are also orthotropic Sexuality is lateral

4 2 2 3 Cynometra travancorica

A lofty tree with an orthotropic main leader axis Compound leaved the leaves are abruptly pinnate Branches orthotropic and sympodial Growth pattern rhythmic

4 2 2 4 Dimocarpus longan

Tree with alternate compound leaves Rough main axis is orthotropic The more or less orthotropic branch axes follow a rhythmic growth pattern

Plate VIII Close up view of Memecylon foliage showing the phyllotaxy and branch arrangement

Plate IX An upper view of *Spondias pinnata* phyllotaxy

4 2 2 5 Diospyros hirsuta

The tree has an orthotropic monopodial trunk with rhythmic growth Branches are plagiotropic wherein the frequency of rhythmic growth can be seen Leaf arrangement in the trunk and branches are distinct

In some individuals plagiotropy is determined late in the development of the branch Plagiotropic axes are usually sympodial

4 2 2 6 Euodia lunu ankenda

The tree possesses axes exhibiting continuous growth differentiated into a monopodial trunk and more or less equivalent branches Branching takes place either continuously or diffusely but continuous growth does not imply a uniform rate of growth Sexuality is lateral and does not affect shoot construction

4 2 2 7 Litsea stocksii

The main axis is an orthotropic monopodium with lateral plagiotropic branches Branch growth is rhythmic A regular fluctuation in leaf size along each branch can be seen Flowers develop where earlier supporting foliage had been present Leaf arrangement is alternate

Plate X A Persea macrantha seedling

4 2 2 8 *Memecylon molestum*

The main leader axis is essentially orthotropic but as age advances it curves abruptly Orthotropic nature is then replaced by a plagiotropic orientation Shoots are sympodial by abortion of the terminal bud Mixed axes are developed subsequently The trunk axis looses its significance Phyllotaxy is spiral

4 2 2 9 *Persea macrantha*

This tree has a monopodial orthotropic trunk which grows rhythmically Orthotropic branches themselves are morphogenetically identical with the trunk Branch development is closely correlated with rhythmic growth of the axis Sexuality is lateral

4 2 2 10 *Spondias pinnata*

The tree has an orthotropic indeterminate trunk with a rhythmically active terminal meristem Tiers of branches are produced each branch complex orthotropic and sympodially branched Branch tiers are very diffuse and in their early development show a repetition of the monopodial growth of the parent trunk before sympodial branching by substitution begins Sexuality is terminal

Discussion

DISCUSSION

5 1 Phenology of the semi-evergreen flora

5 1 1 Flowering

The tropical evergreen vegetation as a whole may hardly show any seasonality but the component plants are more or less periodic in their activity Periodicity is shown in the production of new leaves flowering and other functions The phenological observations carried out for a calendar year for the semi evergreen species reveals that the flowering of these plants is mostly confined to the drier months eventhough a peak was noted in June (Table 2 and Fig 6) Tropical trees have been reported to flower during the stress periods (Kozlowski and Kramer 1979 Hilty 1980) and in the present case too moisture stress would have induced flowering However the semi evergreen tracts might be having a comparatively better soil moisture resources and the phenomenon of flowering could not be entirely attributed to be induced by water stress alone Johson (1992) had observed that plants which flower well in the season are often those which occupy marsh or stream bank communities So the timing of flowering by these species could be due to other ultimate factors apart from the well established proximate factors

Rathcke and Lacey (1985) had correlated a number of abiotic factors with the flowering times like seasonal availability of conditions favourable for pollen transfer availability of pollinators competitive effects on seed set etc The present flowering trend shown could also be a reflection of any one of these attributes or their combinations Another probable reason might be that dry season flowering by these species could be an adaptive mechanism to avoid risking flowers in the rains and thereby losing in competition

5 1 2 Fruiting

Fruiting also peaked during the drier months of the study period (Fig 7) By the time the monsoons had started all the fruits had been set and majority of them were in the forest floor This could be an adaptation by the trees to provide favourable conditions for their early germination since most of the seeds of the tropical evergreen flora are recalcitrant in nature and have very short viability (Nameer 1993) Angevine and Chabot (1979) strongly emphasised that the timing of germination should be under strong selection to occur when conditions will be favourable for seedling establishment The present study revealed a regulated fruiting pattern by these species probably to provide optimal conditions for the seed shed Fruiting timing may also be a reflection of a compromise between the probabilities of predator or pathogen attack at the fruit, seed or seedling stage

5 2 Phenology of the moist deciduous flora

5.2 1 Flushing activity

Most tropical trees produce new leaves in periodic flushes Leaf phenology of the observed deciduous flora indicates that leaves appeared conspicuously in the months of May and November (Fig 4) One of the main peak of leaf change came just at the driest time of the year i e in May and the second one just after the rains in November By producing new leaves prior to the rains trees will be able to expose the new foliage to the photosynthetically active radiation and readily synthesise carbohydrates (Janzen 1967) Also at this period these new leaves are less exposed to the heat waves and can synthesis food materials in advance in the bright sun and make up the loss due to rain clouds in the following months Leaf flushing after the rains could be due to an increased water availability and re appearance of the sun Here, in the present study too the flushing phenomenon exhibited could be satisfactorily explained with these hypotheses

5 2 2 Leaf fall

The deciduous leaf habit was conspicuous during the dry season (Fig 2) Maximum leaf fall was recorded during the dry months of March April and May Water stress is a common feature of the dry seasons wherein availability of moisture would be limited At such circumstances transpiration by the leaves would be detrimental to the survival of the species So the deciduous leaf habit probably evolved as a drought avoidance mechanism (Chabots and Hicks 1988) This offers a plausible explanation for the peak leaf shedding experienced during the summer months Here also in the present study the deciduous habit exhibited by the species could be an adaptive strategy to tide over the water stress periods by cutting down the transpiring surfaces Also water stress could have contributed to the senescence of leaves by favouring the synthesis of abscissic acid (Moore 1980)

5 2 3 Flowering

Flowering by the deciduous tree species was observed to be extended throughout the year and there was no month in which a proportion of the species was not in flower (Fig 3) This follows the generally reported flowering phenomenon of the tropics But a peak could be noticed in April This pronounced maxima has also been reported by Richards (1975) for the tropical forests with a distinct dry season The phenomena of emergence of flowers on the bare branches is characteristically peculiar and conspicuous in the deciduous tree flora (Vinaya and Kumbhojkar 1991) Many species flower when bare of leaves and in trees in which the branches lose their foliage at different times it can be observed that flowering takes place on the bare branches In the present investigation also flowers appeared on the bare branches as the trees had shed their leaves in response to the dry season The phenological cycle was observed to start with leaf fall phase followed by the blossoming phase Whitmore (1984) attributes an ecological significance to the flowering when the crown is bare Flowering during the leaf fall season has an added advantage The trees are able to show off their flowers and thereby attract pollinators All these could be possible explanations for this particular flowering pattern shown by these moist deciduous species

5 2 4 Fruiting

Fruiting by the deciduous flora too appeared to be in rhythm with leaf shedding Fruits were borne when the branches were bare of foliage They were already dispersed with the onset of monsoons This again may be a probable adaptive mechanism to expose the seeds to the maximum optimum germination conditions due to their suspected viabilities

The fruiting patterns of tropical trees has its bearing on natural and artificial forest regeneration Seeds are most often shed during the dry weather which provides the most suitable conditions for their dispersal (Richards, 1975) In the current study too, all these above said hypotheses could have regulated the dry season fruit production by these moist deciduous vegetation

5 3 Tree architecture and growth

All the species analysed architecturally represented a very homogenous group of trees and had their growing axes differentiated into a main trunk and lateral branches

5.3 1 Tree growth phases

5 3.1 1 Seedling growth

The architectural development of a seedling system with its spatial extension would represent a slow suppression of the dominance of the main axis and be responsible for the construction of the whole plant This dominance is maximum at germination, the axes being without branches as yet and quite often having a very long epicotyl before producing the first leaves The seedlings of all the species analysed also were found to conform to this developmental pattern On germination the seeds produced an orthotropic aerial axis which was unbranched at the beginning of its growth

5 3 1 2 Lateral branch production

The above growth pattern got modified soon Utilizing its organizing power the trunk produced very small and almost horizontal (plagiotropic) branches at first and then more vertical branches (orthotropic) The branches at first similar to the trunk in development then seemed to have acquired a complete morphogenetic independence from the latter (Halle et al 1978) Another important morphogenetic process noticed was the progressive transformation of the initially plagiotropic branches into orthotropic ones Branches turned up as age advanced and followed different patterns This progressive acquisition of orthotropy was also reported by Banchilhon (1969) on Phyllanthus and Vogel (1978) for cocoa This transformation also occurred in branches which were initially not completely horizontal It was noted that as the trees grew all the branches turned up completely and acquired a more acute insertion angle This turning up process was also highly differential and occurred for a variable number of branches, and occurred either in a very short or long period of time Naturally each species had a particular way of exhibiting this development But the turning up pattern was noted to be common for all the species analysed

This typical metamorphosis is modulated by the environment Edelin (1990) reported that a full exposure to light accelerated this transformation Havel (1965) clearly found in Klinki pine that acquisition of orthotropic branches was sooner when the transmitted light was abundant Here also for the tropical flora exhibition of this gradual transition from plagiotropy to orthotropy might be an adaptive mechanism to better expose their foliage to the solar energy However opinions do exist as to this phenomenon is fundamentally endogenous

5 3 1 3 Ramified branch production

As the trees grew it produced larger and more ramified branches effecting a profound change in its physiognomy and architecture This change did not occur in all the species but in most of the moist deciduous trees analysed the young branches were more orthotropic However in the semi-evergreen species analysis revealed the young branches to be plagiotropic initially

In all these species these branching orders increased step by step However the trees were found to acquire orders of branches only after a prolonged period The proportion of small new branches increased and their production became stable after a certain age All the axes were not involved in this ramified branch production but in certain species it was noted that even their trunks were bearing these ramified branches This limb production is the expression of a physiological mature state attained by the tree and may not be as a direct response to the supra optimal conditions of the environment (Edelin 1990) The existence of the ramified branches even in the thick seedling undergrowth of the evergreen tracts confirms this interpretation

5 3 1 4 Crown development

The development of the crown depends firstly on the infrastructure established by the tree and then on the nature and positioning of the reiterated complexes (roughly the branched systems) capable of developing on the tree Through growth and differentiation, these are extended and start exploring the surrounding environment The development of these complexes actually reproduces the initial architecture of the tree

The development pattern followed by all the species was that the first phase of tree growth is slowly replaced by the basic architectural growth units as it were naturally grafted to the tree and then developing from its branches and trunk So the tree crown could be viewed as a constantly renewable population of coherent young trees Their life span shortens, their size decreases and they flower more and more precociously leading the tree towards its death

The development of sexuality interestingly is an intermediate phenomenon having profound but often overlooked influence on vegetative growth Flowering started initially on the ultimate branches of the crown periphery and rapidly spreaded to other branch orders progressively influencing vegetative growth

The crown architecture of all the trees analysed followed this basic mode of development

Summary

SUMMARY

Tropical forests are becoming increasingly important to everyone on Planet Earth irrespective of where they dwell No longer can these vegetation be taken for granted since their very existence has in many tropical countries become doubtful This is despite the fact that the tropical forest harbours probably half of the world s floral and faunal wealth and thus represent a remarkably complex ecosystem with specialised ecological and physiological inter relationships between its various biotic and abiotic components Of particular significance are trees the principal floristic element of this ecosystem which shows very distinct developmental attributes quite different from the species in other geographical zones However an understanding of the complexities viz cycling of energy materials and genetic information and of the life cycles and responses of living organisms is essential for the conservation of the tropical bio diversity

A study was carried out in Pattikad Range of Trichur Forest Division with the idea of gaining more information on the phenological dynamics and tree architectural properties of a few tropical forest tree species

The salient findings are summarised below

1 Phenological patterns are determined partly by genetic and partly by environmental factors A climate cued trigger may be a possible cause for the observed phenodynamics apart from the endogenous control

2 Also the patterning of different phenological cycles could be attributed to site dependent stress conditions

3 The transition from the juvenile to the adult tree phase occurred through progressive architectural metamorphoses

4 The initially plagiotropic branches became orthotropic as the trees grew

5 Ramified branches were subsequently produced

6 Characteristic reiterated complexes were subsequently produced on all these branches which helped to form the crown

7 At a later stage sexuality was initiated which progressively affected vegetative growth

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PHENO-MORPHOLOGICAL STUDIES OF SELECTED TREE SPECIES IN A TROPICAL FOREST ECOSYSTEM

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ABSTRACT OF A THESIS

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ABSTRACT

A pheno-morphological study was carried out in Pattikad Range of Trichur Forest Division Kerala Two groups of ten species each where each group represented the moist deciduous and the semi evergreen tract were used for the present investigations The study was initiated in March 1993 and was continued for a calendar year upto February 1994 The study was pursued with the objectives of supplementing information on the different phenological cycles of the commonly found species of this forest area Along with this the important macromorphological features of these trees were noted An attempt was also done to understand the tree architectural principles of these species

The patterning of the phenological events like flowering, fruiting leaf fall and leaf flushing no doubt are partly under endogenous control However in general the timing of these life cycle events were noticed to follow a climatic cue The deciduous habit exhibited by the study species during the dry weather had an ecological significance because it strongly helped the trees to tide over the moisture limiting summer months Likewise dry season flower and fruit production shown by the species might be a part of a much complex adaptive strategy developed by these species through

the course of competitive evolution Apart from these climatic triggers there exists possibilities of several other external stimuli that might have favoured these important seasonal cycles However the cardinal factor effecting these events would be the climatic factors through its direct and indirect influences on the physiological mechanisms of these woody plants Regarding tree architecture it was noted that all the species build up through a progressive duplication of their basic architectural units This architectural metamorphosis continued from seedling stage upto the death of the tree Branch production and initiation of sexuality were intermediate events However, the free expression of the architecture was found drastically affected possibly due to the different stresses that perennial woody species encounters in its long life span